Reptiles in Resorts: The Responses of Reptiles to Ski-related Disturbances in Subalpine Environments

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Declaration

This thesis is my own work, except where otherwise acknowledged

(see Preface and Acknowledgements).

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Preface

This thesis is structured as a series of connected papers that have been published, accepted, or submitted for publication at the time of thesis submission. All papers were intended as stand-alone pieces of work. For this reason, there is some unavoidable repetition between chapters, for example in the nature of the background material and the description of study areas.

In line with The Australian National University's College of Medicine, Biology and Environment guidelines for 'Thesis by Compilation', a Context Statement has been provided at the beginning of this thesis. The Context Statement is not intended to be a complete literature review, but rather a framework for understanding the relationships between all aspects of the research. Paper I provides a detailed review of literature concerning the effects of ski resorts on wildlife, and subsequent paper each present a review of literature relevant to the research focus of the paper.

I performed the majority of the work for the papers that form this thesis, including developing research questions and experimental designs, data collection and analysis, and drafting manuscripts. However, at each stage of the design, execution and write up of research, I was advised by my supervisors (David Lindenmayer, Ken Green, Mellesa Schroder and Damian Michael) and collaborators (Jeff Wood and Will Osborne). The addition of different co-authors to each paper reflects contributions to the conceptualization of ideas, collection and analysis of data, and editing of manuscripts. Specific contributions of co-authors to each paper are outlined below. Other assistance for each paper is acknowledged at the end of each paper.

Paper I: *Sato, C.F., Wood, J.T. & Lindenmayer, D.B. (2013) The effects of winter recreation on alpine and subalpine fauna: A systematic review and meta-analysis. PLoS ONE 8(5): e64282.*

Review conceptualization & design: CFS, DBL, JTW; Data extraction: CFS; Data analysis: CFS, DBL, JTW; Manuscript drafting: CFS; Manuscript editing & preparation: CFS, DBL, JTW

Paper II: *Sato, C.F., Wood, J.T., Schroder, M., Green, K., Michael, D.R. & Lindenmayer, D.B. (2013) The impacts of ski resorts on reptiles: A natural experiment. Animal Conservation. doi : 10.1111/acv.12095*

Experimental conceptualization & design: CFS, DBL, DM, JTW, KG, MS; Field work & data collection: CFS, KG, MS; Data analysis: CFS, JTW; Manuscript drafting: CFS; Manuscript editing & preparation: CFS, DBL, DM, JTW, KG, MS

Paper III: *Sato, C.F., Wood, J.T., Schroder, M., Green, K., Osborne, W.S., Michael, D.R. & Lindenmayer, D.B. (2014) An experiment to test key hypotheses of the drivers of reptile distribution in subalpine ski resorts. Journal of Applied Ecology 51: 13-22.*

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Paper IV: *Sato, C.F., Wood, J.T., Schroder, M., Michael, D.R., Green, K. & Lindenmayer, D.B. (in press) Designing for conservation outcomes: The value of remnant habitat for reptiles on ski runs in subalpine landscapes. Landscape Ecology.*

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Paper V: *Sato, C.F., Schroder, M., Green, K., Michael, D.R., Osborne, W.S. & Lindenmayer, D.B. (2014) Managing ski resorts to improve biodiversity conservation: Australian reptiles as a case study. Ecological Management & Restoration 15: 147-154.*

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Second (and no less important), thank you to the Fenner School of Environment and Society and the National Parks and Wildlife Service (Snowy Mountains Region) for financially supporting my research through the *Glenn Sanecki Alpine Scholarship*.

Third, I would like to thank the staff at the New South Wales ski resorts for assisting me with my research: Euan Diver and Thredbo ski resort for transportation around the mountain; Tanya Bishop and Perisher ski resort for accommodating my requests to postpone summer slashing of ski runs; Rolf Klicker and Charlotte Pass ski resort for minimising disturbance to my sites and for their keen interest in my work. I would also like to thank the numerous people who helped me collect data, who carried roof tiles across the mountains, and who kept me company over the summer months: Laura Rayner, Mel Schroder, Drew Geary, Kathleen Sato, Will Osborne, Sam Nicholson, David Perfrement and Glenn Normand.

Finally, I would like to thank my family and friends for their support and for keeping me sane during 'the experience' – particularly Laura Rayner, who read many drafts, cooked many meals and picked me up many times when the going was tough; Drew Geary, who supported my initial move from Sydney to Canberra and my desire to 'do a PhD'; Bo Ok, who has been around since forever and has the greatest regard for my work (even if she doesn't really 'get' it!); and my Fenner family past and present: Dejan Stojanovic & Ingrid Stirnemann (it seems so long since we shared the dreaded internal office), Matt 'going off his face' Brookhouse, Pia Lentini, Karen Ikin, Martin Westgate, Crid Fraser, John Stein, Brett Howland, Juliana Lazzari, Annabel Smith, Alessio Mortelliti, Philip Barton, Geoff Kay, Kevin MacFarlane, John Evans, Claire Foster, Kate Grarock, Ben Scheele, Walter Reinhardt and Sarah Goldin, While there were some rocky patches for me, I can safely say that you all greatly enriched the experience and made me realise countless times over why I left the high school classroom for the great outdoors!

Abstract

The expansion of ski resorts has been recognised as a threat to alpine-subalpine ecosystems that can irreversibly damage native vegetation and negatively affect fauna. However, ski tourism contributes substantially to the economy of many countries. Hence, it is in the interest of those nations to continue developing alpine-subalpine areas to meet the demands of patrons. Due to this pressure, species losses - particularly of threatened endemics - could occur without the implementation of management plans informed by empirical research. However, limited peer-reviewed research has investigated the effects of ski-related disturbances on wildlife, especially reptiles.

In this thesis, I investigated reptile distribution patterns in and around ski resorts, as well as potential drivers of these patterns. Using a combination of trapping and active searching, I found that: 1) reptiles were largely absent from ski runs; 2) reptiles occurred in patches of remnant woodland/forest retained on ski runs, particularly in the edges of patches close to continuous forest; 3) reptiles with specific habitat requirements (specialists) were less tolerant of disturbance than reptiles with broader habitat requirements (generalists).

Investigations into the potential factors driving these patterns indicated that vegetation composition, habitat structural complexity, predation risk and thermal regimes contributed to observed reptile distributions. Each reptile species studied was associated with either a compositional feature (e.g. specific alpine-subalpine plant species) or structural feature (e.g. woody debris or large rocks) of alpine-subalpine habitats. Hence, we argue that alterations to these habitat attributes when creating ski runs will supress lizard abundances in these areas. This is particularly evident for ski runs, which reptiles generally avoided. The low structural complexity on ski runs offered reptiles no refuge from elevated predation levels in ski resorts, or the extreme thermal regimes recorded on ski runs. However, the negative effects of ski-related

habitat fragmentation and habitat loss on reptiles may be mediated by the retention of remnant habitat patches on ski runs. I found that remnant patches, regardless of size, are capable of supporting similar densities of reptiles to those found in continuous forest. This may be due to the altered thermal conditions available at the edges of remnant patches. Thermal regimes in edges were warmer than those of core vegetated habitats, but cooler than those on ski runs, potentially providing reptiles with a favourable environment for thermoregulation.

Based on my investigations, to improve the conservation outcomes of alpine-subalpine reptiles in ski resorts, I recommend that: i) intensive disturbances be restricted to already highly modified areas of ski resorts; ii) existing native vegetation and habitat structures be retained wherever possible during ski developments; and iii) structural complexity be re-established at highly modified sites through revegetation and the cessation of mowing. In providing these recommendations, I emphasize that: 1) effective management strategies targeting the conservation of reptile diversity in alpine-subalpine landscapes require an understanding of *both* the distribution patterns and the drivers that determine those distributions in these landscapes; and 2) there is an urgent need for more empirical research to inform current, and future, management of wildlife in alpine-subalpine areas.

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Context Statement

Introduction

Alpine and subalpine ecosystems occupy only a small proportion of the Earth's terrestrial landmass (approximately 7.9% excluding Antarctica; Körner, Paulsen and Spehn, 2011) but occur on every continent. These ecosystems are topographically and environmentally varied (Martin, 2013; Nagy and Grabherr, 2009), leading to a diversity of local microclimates (Nagy and Grabherr, 2009) that support rich and often highly endemic communities of plants and animals (Körner, 2004). However, due to low ambient temperatures limiting plant growth (Williams, 1987) and shortening both growing and breeding seasons (Nagy and Grabherr, 2009), alpine communities are particularly sensitive to, and recover slowly from, disturbance (Rixen, 2013).

Over the last few decades, high mountain environments have become increasingly popular tourist destinations, particularly for winter recreation (Hudson, 1998; Pickering *et al.*, 2003). There was a rapid expansion of the ski industry from the 1970s onward (Hudson, 1998). For example, in Japan alone, 650 ski fields have opened since 1970 (Kureha, 2008). Today, there are around 6000 ski resorts and ski areas in 70 countries across the world (Vanat, 2012) that contribute significantly to local economies (e.g. $1.561 billion AUD in 2011 for Austalia, ARCC, 2012; and 4.5% of the gross national product each year for Austria; Breiling, 1998).

The benefits afforded to local economies can have a considerable cost to the environment. Ski resorts disturb alpine and subalpine environments because the construction of suitable skiing terrain requires the clearing of vegetation (Ries, 1996), removal of rock and logs (Hadley and Wilson, 2004; Ries, 1996), compaction of soils (Burt and Rice, 2009), and the seeding of cleared ski runs with exotic grasses (Tsuyuzaki, 1994). These types of disturbances are generally acknowledged to be negative for plants (Burt and Rice, 2009; Rixen, 2013; Wipf *et*

al., 2005) and animals (Amo, Lopez and Martin, 2007; Laiolo and Rolando, 2005; Sanecki *et al.*, 2006; Schatz, 1983). However, rigorous scientific research regarding the effects of ski resorts and ski-related disturbances on wildlife is limited (Hadley and Wilson, 2004; Rolando *et al.*, 2007), particularly for reptiles, amphibians and invertebrates (except arthropods; Sato, Wood and Lindenmayer, 2013). Without an understanding of the effects that ski resorts have on wildlife, and the drivers underpinning those effects, it is challenging to implement effective conservation actions for biodiversity (Christensen *et al.*, 1996). Indeed, for reptiles, management strategies aimed at mitigating the negative effects of ski-related disturbances have been largely overlooked by the managers of ski resorts (e.g. PBPL, 2002; RMOW, 2007).

In Australia, the lack of specific conservation actions for reptiles in ski resort plans is a concern because alpine-subalpine zones support a relatively diverse assemblage of reptiles (18 species; Green and Osborne, 2012), of which two species, the Alpine she-oak skink (*Cyclodomorphus praealtus*) and the Guthega skink (*Liopholis guthega*), are restricted to elevations above 1500 m (which makes up less than 0.15% of Australia's terrestrial landmass; Green and Osborne, 2012; Williams and Costin, 1994). Moreover, both *C. praealtus* and *L. guthega* are listed as endangered under the *Environmental Protection and Biodiversity Conservation Act 1999*, and ski-related disturbances are highlighted as a significant threat to the persistence of these species in Australian alpine-subalpine environments (TSSC, 2009; TSSC, 2011). To assist the conservation of *C. praealtus* and *L. guthega* (as well as other reptile species occurring in the Australian high mountain environments), the overarching aim of my research was to understand the effects that ski-related disturbances have on reptiles through: 1) identifying current patterns of landscape use by reptiles in disturbed (ski resort) and undisturbed (National Park) alpine-subalpine environments; and 2) determining the influence of important biotic and abiotic factors such as predation, vegetation composition, thermal regimes and structural complexity, in driving current reptile distribution patterns.

Overview of Aims and Methodologies

In Paper I, I aimed to consolidate current, peer-reviewed knowledge regarding the global effects of ski resorts on wildlife using systematic review and meta-analytic techniques, thus establishing a baseline for the types of effects likely to occur in Australian ski resorts. In Papers II-IV, I explicitly tested the effects of ski-related disturbances on reptiles, as well as the potential drivers of those effects, using landscape-scale experiments. I conducted these investigations in and around Perisher Blue, Charlotte Pass and Thredbo ski resorts in New South Wales, Australia. The reptile survey plots varied in altitude from 1400 m to 2050 m, and across this range a variety of vegetation communities were present including Snow Gum (*Eucalyptus niphophila*) woodlands, wet heathlands (*Epacris* spp., *Baeckea utilis*) and dry heathlands (*Kunzea muelleri*, *Nematolepis ovatifolium*, *Prostanthera cuneata*), sod tussock grasslands (predominantly *Poa costiniana* and *Rytidosperma nudiflorum*), and bog communities (*Epacris* spp., *Sphagnum cristatum*, *Richea continentis*) (Costin *et al.*, 2000). I focussed my surveys in three, structurally distinct vegetation types: snow gum woodlands or *E. delegatensis-E. dalrympleana* forests that intergrade with *E. niphophila* woodlands, dry heathlands and grasslands. This allowed me to maximise opportunities to study a diversity of reptile species, and also test a broader range of ecological theories (e.g. habitat fragmentation theory, structural complexity theory and the specialist-disturbance hypothesis). The relationships between the concepts tested in this thesis are illustrated in Figure 1.

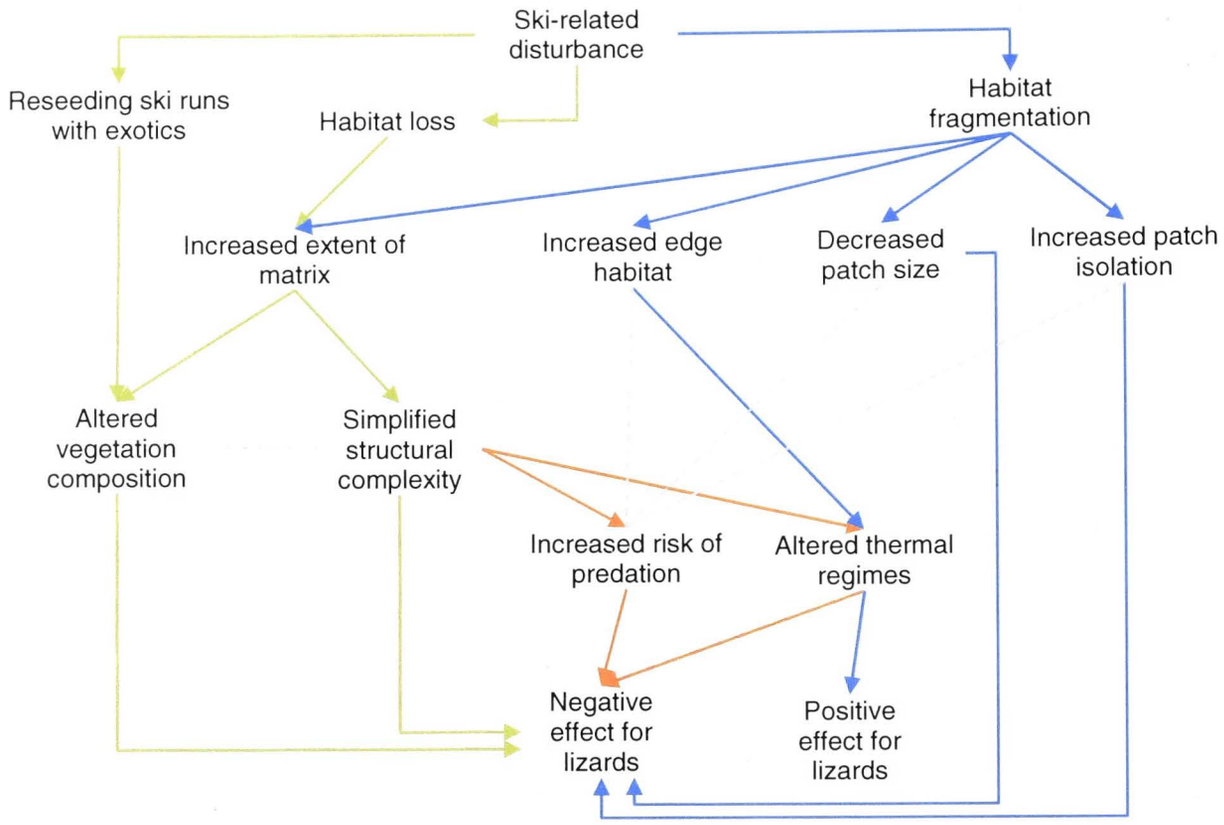

Figure 1. Conceptual diagram illustrating the links between theories tested in this thesis. Coloured lines represent theories tested in different papers: green = Paper II, orange = Paper III, blue = Paper IV. Dashed grey lines represent relationships that were not tested in this thesis.

In Paper II, I investigate the broad distribution patterns of reptiles in three subalpine habitat types (woodland, heathland and grassland) in both ski resorts and National Park. Using Generalised Linear Modelling (GLM), Hierarchical Generalised Linear Modelling (HGLM) and Canonical Correspondence Analysis (CCA), I examine the effects of ski-related disturbances on generalist reptiles (i.e. species with broad ecological niches including dietary and habitat requirements) and specialist reptiles (i.e. species with narrow ecological niches), as well as the importance of vegetation composition and habitat structural complexity in determining habitat selection by reptiles.

Prompted by the findings of Paper II, in Paper III, I examine biotic and abiotic factors that may underpin the avoidance of ski runs by reptiles. Here, I employ an intervention experiment to determine how a resort management strategy, mowing (i.e. simplification of structural complexity), affects predation risk and thermal regimes (two important factors influencing the survival of reptiles worldwide; Martin and Lopez, 1999; Webb and Whiting, 2005).

In the final experimental paper, Paper IV, I investigate the effects of ski-related disturbances on reptile distributions in the framework of habitat fragmentation theory. Using HGLMs, I examine the effects of patch size, patch isolation and edge effects on lizard density. Concurrently, I use GLMs to examine how habitat fragmentation and habitat loss affect thermal regimes, and whether modifications to thermal regimes contribute to the patterns of lizard distribution observed at Thredbo ski resort.

Summary of Findings

Paper I: The effects of winter recreation on alpine and subalpine fauna: A systematic review and meta-analysis.

The systematic review I conducted in Paper I indicated that the effects of ski-related disturbances on animals are more likely to be negative or neutral, than positive. The meta-analysis supported this finding, revealing lower faunal diversity and richness in areas affected by ski-related disturbances. More importantly, the systematic review revealed that there are many gaps in our knowledge regarding the effects of ski-related disturbances on fauna and markedly so for reptiles in Australian ski resorts. In particular, we have a limited understanding of: 1) the distribution patterns of reptiles inside and outside ski resorts (in Australia and elsewhere); 2) what factors may be contributing to the distributions of reptiles inside and outside ski resorts; and 3) whether features of ski resort design, such as patches of remnant vegetation retained on ski runs, are used by reptiles allowing for dispersal throughout the landscape – or whether the creation of ski runs is a barrier to movement for these animals.

Paper II: The impacts of ski resorts on reptiles: A natural experiment.

Paper II highlighted the generally negative effects that ski-related disturbances have on reptile abundance in Australian ski resorts. Lizards generally absent from ski runs, and disturbed heathlands and woodlands support lower numbers of specialist lizards (i.e. those species with specific habitat requirements) than undisturbed habitats. Generalist lizards appear more tolerant

to disturbance when habitat structural complexity is maintained, occupying disturbed woodlands and heathlands in similar densities to undisturbed habitats. Given that each lizard species studied was positively associated with compositional or structural features of the environment, the magnitude and extent of alterations to these habitat attributes when creating ski runs or other ski-related infrastructure is likely to influence the degree to which lizard abundances are affected in disturbed ski resort areas.

Paper III: An experiment to test key hypotheses of the drivers of reptile distribution in subalpine ski resorts.

Paper III showed that ski resort management practices which simplify habitat structural complexity also modify the important drivers of reptile distribution. The removal of vegetation structural complexity through mowing resulted in higher rates of predation on plasticine lizard models. While the use of plasticine lizard models may overestimate rates of predation due to the inability for the models to attempt escape, the result is still relevant because: 1) the distribution of attacks on the models suggest that avian predators treated the models as real prey items (i.e. majority of bite marks occur on the head and trunk), consistent with other studies using plasticine models (e.g. Webb and Whiting 2005); and 2) the models mimic the freezing response real lizards have to predators (Daly et al. 2008). Hence, plasticine models are indicative of potential predation risk in 'real-world' scenarios and provide an indication of comparative predation risk in habitats of differing structural complexity. In addition to altered predation risk, mowing grasses on ski runs markedly altered thermal regimes. Crucially, mown ski runs had higher maximum ground temperatures that frequently exceeded the recorded critical maximum body temperatures of Australian subalpine lizards. Thus, mowing has the potential to render exotic grass ski runs unsuitable for thermoregulatory purposes for a large proportion of reptile active periods. Together, modifications of the thermal environment and elevated predation risk appear to contribute, potentially additively, to the avoidance of ski runs by reptiles.

Paper IV: Designing for conservation outcomes: The value of remnant habitat for reptiles on ski runs in subalpine landscapes.

In Paper IV, the number of lizards observed differed between habitat types (ski runs vs. forested areas) and with patch isolation, but not with patch size. Additionally, the edges of patches supported more lizards than any other areas of habitat. These patterns of lizard distribution can be explained, to a certain extent, by the differing thermal regimes. Ski runs had higher ground surface temperatures than any other habitat type, precluding their use for a considerable proportion of the activity period of a lizard. In comparison, edges were characterised by lower temperatures than ski runs, but higher temperatures than the core of forested areas, potentially providing a favourable environment for thermoregulation. Paper IV emphasises that habitat fragmentation, through the creation of ski runs, has a negative effect on reptiles in high mountain environments. However, it also indicates that patches of remnant vegetation retained on ski runs are of value to lizards and may, in part, mitigate the negative effects of habitat fragmentation.

Paper V: Managing ski resorts to improve biodiversity conservation: Australian reptiles as a case study.

Paper V is intended as a summary and concluding chapter for the thesis, but also a management report that can be used by practitioners to improve conservation outcomes for reptiles in Australian ski resorts. In this paper, I draw together current knowledge on the effects of ski-related disturbances on reptiles, including all the findings from my thesis research. Based on this information, I recommend management strategies to facilitate the persistence of reptiles in Australian ski resorts, such as the retention of native vegetation, the revegetation of ski runs with native grasses and low shrubs, and the use of linear habitat strips (i.e. submerged rocks and logs) to connect patches of habitat isolated by ski runs. I also highlight the importance of taking a precautionary approach to the conservation of reptiles at high altitudes, given the sensitivity of the ecosystems to disturbance, the potential impacts of climate change on these environments, and the current limitations in our understanding of the ecology of this assemblage.

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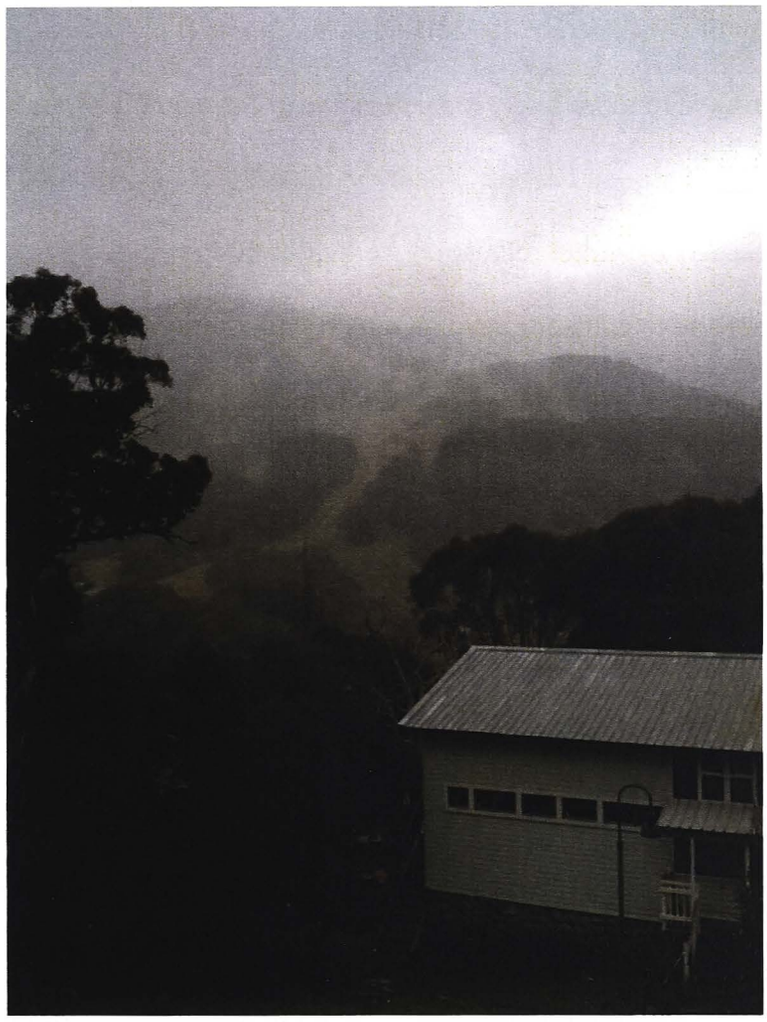
PAPER I: The Effects of Winter Recreation on Alpine and Subalpine Fauna: A Systematic Review and Meta-analysis



Ski-related disturbances are generally accepted to have negative effects on alpine and subalpine fauna. However, to date, there has been no systematic review of key threatening processes influencing biodiversity in alpine-subalpine systems, particularly in regards to immediate and direct human-driven impacts potentially arising from tourist resort development and extension. In this paper, I consolidate current, peer-reviewed knowledge regarding the global effects of ski resorts on wildlife, thus establishing a baseline for the types of effects likely to occur in Australian ski resorts.

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Abstract

The ski industry is often perceived as having a negative impact on sensitive alpine and subalpine communities. However, empirical evidence of such impacts is lacking. We reviewed the available literature from the last 35 years to quantify the reported effects of winter recreation on faunal communities. Overall, using one-sample binomial tests ('sign tests') we found that the effects of all types of winter recreation-related disturbances (i.e. ski runs, resort infrastructure and winter tourism) were more likely to be negative or have no effect, than be positive for wildlife. More specifically, in Europe, where the majority of the available research was conducted, the impacts of winter recreation were most often negative for fauna. In terms of specific taxa, birds and to a lesser extent mammals and arthropods, responded negatively to disturbance. Results from our meta-analysis confirmed the results from our binomial tests. Richness, abundance and diversity of fauna were lower in areas affected by winter recreation when compared with undisturbed areas. For most regions and taxa, however, empirical evidence remains too limited to identify clear impacts of winter recreation. We therefore conclude that the majority of ski resorts are operating in the absence of knowledge needed to inform effective strategies for biodiversity conservation and ecologically-sound management. Thus, there is an urgent need for more empirical research to be conducted throughout this increasingly threatened ecological community, especially given the indication from the available literature that fauna often respond negatively to winter recreation.

Keywords: *alpine environments, ski-runs, ski resorts, subalpine environments, tourism, winter sports.*

Introduction

Alpine ecosystems are significant for biodiversity [1,2,3] but only cover between 5.2-7.9% of the Earth's terrestrial landmass (excluding the Antarctic landmass; [4,5]). Many alpine and subalpine environments support highly endemic communities of taxa [6,7] such as reptiles [8], birds [9,10] and invertebrates [11,12]. These ecosystems are also thought to be sensitive to human development [13,14,15,16], domestic livestock grazing [17], invasive species [18] and intensive wildfires [19]. In addition, these environments are expected to be significantly affected by climate change [20,21]. Under a conservative scenario of only 1°C global temperature increase, some authors predict a 150 m retraction of the snow line up the mountains [22,23,24]. Severe global warming scenarios (IPCC scenario A1B; [20]) predict that global temperatures may increase by 1.5-2.4°C by 2050 [20,24]. This could see snow lines retract by as much as 220-360 m upslope (based on figures provided by [20,22,23,24]). Indeed, snow line retractions may be even more severe than predicted when other factors such as snow-pack variability, North Atlantic Oscillations and El Niño/La Niña are considered [25,26].

The ski industry is already implementing climate adaptation strategies (e.g. artificial snow making and the introduction of high capacity ski lifts that can access higher elevation ski runs) to increase longevity of winter tourism activities [20,22,27]. These adaptation strategies may adversely affect fauna [20] by limiting the area of undisturbed habitat available for endemic species, especially those sensitive to human disturbances (e.g. Mountain Pygmy Possum, *Burramys parvus*, in south-eastern Australia [28,29]).

Effective management and conservation of alpine and subalpine systems requires high quality empirical information to guide policy and on-the-ground management interventions. Yet, major knowledge gaps remain in many areas ranging from the biology of alpine organisms [30,31] to the effects of stressors, such as human-induced environmental change, on populations and communities [11,32,33,34].

To date, there has been no systematic review of key threatening processes influencing biodiversity in alpine-subalpine systems, particularly in regards to immediate and direct human-driven impacts potentially arising from tourist resort development and extension. Yet, this information is critical to guiding effective management and evidence-based policies. To address this major knowledge gap, we have conducted a targeted and detailed systematic review and meta-analysis of the global literature to quantify the impacts of ski tourism and ski resort infrastructure on alpine-subalpine wildlife. To this end, we asked the following key questions:

1) Which taxa appear to be most heavily affected by alpine and/or subalpine development?
2) Are there regional patterns in biotic response with some areas experiencing greater impact than others?
3) Is the nature of the impact consistent across different winter recreation-related disturbances?

Methods

For the purposes of this review, we classify alpine and subalpine areas using the globally applicable definitions provided by Löve (1970; [5]). She defines an alpine area as the zone above the limit of physiological tree growth (the treeline) and a subalpine area as the natural belt that lies between the treeline (at its upper limit) and the closed montane forest (at its lower limit).

We focused this review on studies that generated empirical data on the impacts of human disturbances on terrestrial vertebrate and invertebrate taxa of alpine and subalpine areas around the world. Human disturbances included ski-related developments (such as roads, buildings and ski-lifts; henceforth termed 'Resort Infrastructure'), direct mountain management and modification (such as slope and snow grooming; henceforth termed 'Ski Runs'), and direct human impact from winter recreational sports (including snow-shoeing, skiing, snowboarding and over-snow vehicle use; henceforth termed 'Winter Tourism').

Literature Search

Due to the broad, geographical nature of our review (see Figure 1), obtaining all the "grey" literature on the impacts of ski resorts on alpine and subalpine fauna was not feasible. As such, we only used the peer-reviewed primary literature as identified via electronic databases for our analyses.

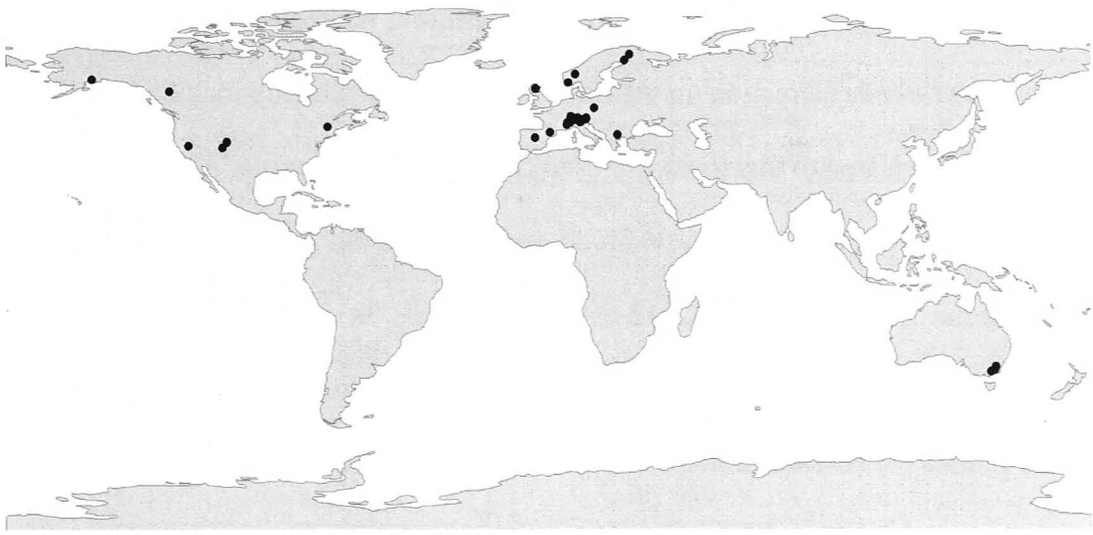

Figure 1. Global distribution of studies (n = 41) that investigated the effects of winter recreation on wildlife.

We searched four major electronic databases - Web of Science (1945-present), Zoological Record Plus (1978-present), ProQuest: Science and Technology Databases (1967-present) and CAB Abstracts (1973-present) - on the 16th April 2012 using the following search string: ((ski slope* OR ski lift* OR ski run* OR ski piste* OR piste* OR ski resort* OR "ski develop*") OR ("snow* sport*" OR ski sport* OR winter sport* OR "winter recreation") OR ("winter tourism" OR "ski tourism" OR "nature tourism" OR snow tourism) OR ("alpine habitat fragment*" OR "alpine modification" OR devegetated matrix) OR ("subalpine habitat fragment*" OR "subalpine modification" OR devegetated matrix) OR (snow AND alps)) AND (fauna* OR (bird* OR avifauna*) OR mammal* OR (reptil* OR lizard*) OR (frog* OR amphib*) OR (invertebrat* OR insect*)).

We used different combinations of search terms based on the requirements or limitations of each database. No constraints on year of publication or language of publication were imposed on the database searches. We also examined additional, relevant articles collected opportunistically over the previous year.

Extraction of data for analysis

Our systematic literature search was designed to find studies related to the effects of ski resort infrastructure and winter recreation on wildlife. To ensure that we only included articles in the review specifically related to this topic, we used two levels of screening. At the first level of screening, we read titles and abstracts, excluding articles that did not satisfy at least two of the following criteria: 1) Focus on fauna, 2) Mention ski resorts, ski infrastructure or winter sports, 3) Concentrate on alpine or subalpine environments. Full text articles were obtained for all the articles that passed the first level of screening. At the second level of screening we read entire articles, excluding those that did not: 1) include original research focussing on effects of winter recreation-related disturbances on fauna, 2) contain usable, empirical data, or 3) provide statistical analysis of data. At each level of screening, we recorded the number of articles identified and the number of studies included and excluded according to the Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) Statement (see Figure 2).

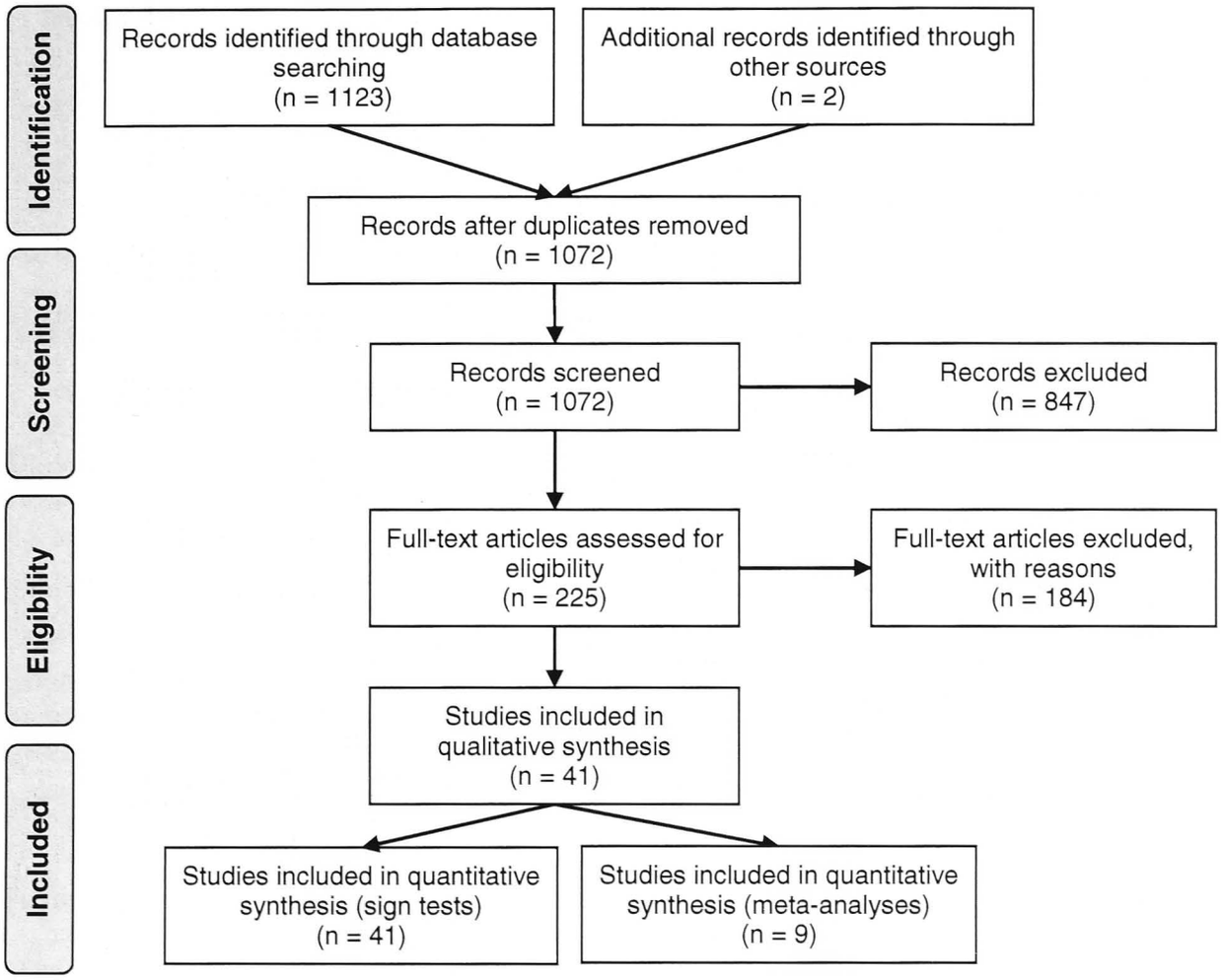

Figure 2. PRISMA Literature Search Flow Diagram.

For each of the 41 papers included in the final analysis (see Table 1, Reference List S1), we posed the following questions. (1) In which country was the study conducted? (2) In what year(s) was the study conducted? (3) What taxonomic group was examined? (4) What type(s) of winter recreation-related disturbance was examined? (5) What measurements were taken to determine the effect of winter recreation? (6) What overall effect on the fauna was observed (as concluded by the author)? (7) What specific effect on fauna was observed for each measure recorded in the study? (8) Were any management recommendations included? We also assigned each paper an experimental design/data quality category (I-IV), as outlined in Table S1. We show the proforma used to extract information from retained articles in Table S1 and PRISMA Checklist in Checklist S1.

Table 1. Details of the 41 studies* investigating the impacts of winter recreation on alpine and subalpine fauna.

Author	Country	Taxa
Amo et al. (2007)	Spain	Reptile
Arlettaz et al. (2007)	Switzerland	Bird
**Ballenger & Ortega (2001)	USA	Bird
Baratti et al. (2000)	Italy	Arthropod
Braunisch et al. (2011)	Switzerland	Bird
Broome (2001)	Australia	Mammal
**Caprio et al. (2011)	Italy	Bird
Caravello et al. (2006)	Italy	Annelid
Foissner et al. (1982)	Austria	Protozoan
Goldstein et al. (2010)	USA	Mammal
Goodrich & Berger (1994)	USA	Mammal
Green (2000)	Australia	Mammal
Hadley & Wilson (2004a)	USA	Mammal
Hadley & Wilson (2004b)	USA	Mammal
Haslett (1991)	Austria	Arthropod
Haslett (1997)	Germany	Arthropod
Jokimaki et al. (2007)	Finland	Bird
**Keßler et al. (2012)	Austria & Germany	Arthropod
Krebs et al. (2007)	Canada	Mammal
Kübelböck & Meyer (1981)	Austria	Annelid
**Laiolo & Rolando (2005)	Italy	Bird
Lüftenegger et al. (1986)	Austria	Protozoan + Nematode
Mansergh & Scotts (1989)	Australia	Mammal
**Mincheva et al. (2009)	Bulgaria	Nematode
Morrison et al. (1995)	USA	Mammal
**Negro et al. (2009)	Italy	Arthropod
**Negro et al. (2010)	Italy	Arthropod
Nellemann et al. (2000)	Norway	Mammal
Patthey et al. (2008)	Switzerland	Bird
Reimers et al. (2003)	Norway	Mammal
**Rolando et al. (2007)	Italy	Bird
Sanecki et al. (2006)	Australia	Mammal
Shine et al. (2002)	Australia	Reptile
**Strong et al. (2002)	USA	Arthropod
Szymkowiak & Gorski (2004)	Poland	Arthropod
Thiel et al. (2007)	Germany + France	Bird
Thiel et al. (2008)	Germany	Bird
Thiel et al. (2011)	Germany + Switzerland	Bird
Ukkola et al. (2007)	Finland	Mammal + Bird
Watson (1979)	Scotland	Mammal + Bird
Watson & Moss (2004)	Scotland	Bird

*Complete reference details provided in Reference List S1;
** indicates studies included in the meta-analyses.

Reporting of results

We collated the information extracted from each paper in qualitative tables and presented these results using simple tables and bar charts. As 20 different measures of biotic response were reported across the included studies, we recorded the overall effect identified by each individual paper, but also pooled logical subsets of biotic response measures to create four composite categories. In doing so, we could analyse the effects of winter recreation-related disturbances on specific biotic responses of fauna. The four composite categories analysed were:

1) *population and community descriptors*: measures used to describe a population or community of animals (e.g. abundance, diversity, richness and community composition);
2) *population viability measures*: measures that may contribute to the persistence and viability of populations (e.g. breeding success, recruitment and survival);
3) *fitness measures*: measures that may contribute to the survival of an individual (e.g. body condition, parasite load and sprint speed); and
4) *'other' measures*: measures that did not fall under one of the above categories (e.g. habitat use, frequency of occurrence and predicted presence).

Examples of the types of results we recorded as 'positive effect', 'negative effect' and 'no effect' for each of the composite categories are provided in Table S2.

To test the hypothesis that human-generated disturbances were equally likely to have a positive or negative effect on fauna, we used data from studies that demonstrated clear positive or negative effects on fauna and omitted from analysis ambiguous results (i.e. 'no effect' or variable results). We calculated the proportion of studies that had a positive effect on the focal species or focal community and used one-sample binomial tests ('sign' tests; [35]) to assess whether this proportion was significantly different from 0.50. We performed separate one-sample binomial tests for each of the data sets (continents, taxa, and specific types of winter recreation-related impacts). Data sets with sample sizes of less than six were omitted from our analysis as the statistical power to detect significant differences is likely to be inadequate below this level [36].

The use of one-sample binomial tests allowed us to statistically test broad hypotheses about the effects of winter recreation on fauna despite the variability in the measures reported among included articles [35]. We also conducted a meta-analysis to determine the effect of winter recreation on fauna. We found that only three measures – richness (n = 8), diversity (n = 6) and abundance (n = 7) - had a sufficient number of studies (five or more) that provided the required

information (means, standard deviations and sample sizes) to calculate an overall effect size using weighted Hedges' *d* [37]. To make these effect sizes ecologically meaningful, we first standardised the reported data so that each study only yielded means and standard deviations for specific taxonomic assemblages (e.g. birds, mammals, arthropods etc.) Thus, for those studies where information was provided for individual species or individual study areas, we combined site-level or species-level means and standard deviations for each measure according to formulae provided by Borenstein et al. [35, p.222]. We then calculated the effect sizes for each study using weighted Hedges' *d*, as well as an overall effect size of winter recreation for each measure by combining the effect sizes across studies (see [37, p.16]). We assessed winter recreation as having a statistically significant effect on a given measure if the 95% confidence interval (CI) did not overlap zero. We conducted all meta-analyses using Genstat 15 (VSN International Ltd).

Results

Our systematic literature search retrieved 1072 articles that were potentially relevant to the review. Of these, we found 847 abstracts to be unrelated to the impacts of winter recreation on wildlife and so we rejected them. We read the remaining 225 articles in full and found a further 184 did not meet our inclusion criteria. Thus, we retained 41 articles for our final analysis (Figure 2).

The 41 articles included in our analysis were sourced from 25 different journals. The majority were published in *Biological Conservation* (14.6%), *Journal of Wildlife Management* (14.6%), *Journal of Applied Ecology* (9.6%) and *Biodiversity and Conservation* (7.3%). All other journals published two or fewer articles related to the impacts of winter recreation on fauna. In addition, the number of publications increased over time from just one during the 1970s to 25 during the period 2000-2009 (Figure 3). Seven studies have been published since 2010 (Figure 3).

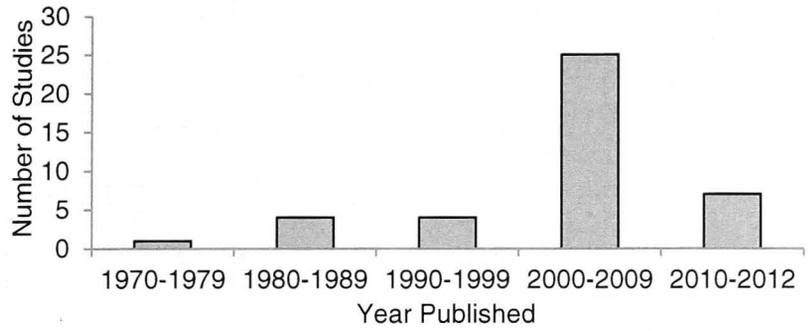

Figure 3. Publications by decade. The number of studies (n=41) published by decade, investigating the impacts of winter recreation on fauna from 1970 to mid-2012.

Generally, the experimental design and data quality of papers was high according to the criteria in Table S1. Most studies (34/41) were assigned to category one or two (i.e. controlled studies with adequate replication). The remainder fell into category three (7/41; replication was not adequate). No study fell into category four (i.e. control was absent).

Geographical Area

Most studies were conducted in Europe, predominantly in Italy, Austria and Germany (Table 2). The remainder were conducted in North America (primarily in the USA) and Australia (Table 2). No studies were completed in South America, Asia or Africa. The proportion of available studies in the peer-reviewed literature conducted in Europe and North America approximates the global proportion of ski resorts in these areas i.e. European studies make up 68% of included articles and European ski areas represent approximately 62% of all ski areas [38]. In comparison, Asia and South America were clearly under-represented in the peer-reviewed literature considering the proportion of ski areas located in these regions (Table S3). On the other hand, Australia was over-represented, contributing 12.2% of peer-reviewed studies but representing only 0.2% of all ski areas (Table S3).

In terms of management, Australian and North American studies provided recommendations in the majority of their publications (4/5 and 6/8 respectively), whereas European studies did so in only 60.7% of publications (17/28). No temporal bias was apparent in the provision of recommendations for each region (Table S4).

Table 2. Numbers of published studies that investigated the impacts of winter recreation on wildlife.

Category			Total	Negative	No Effect	Positive
Continent						
	Europe		**28**			
		Austria*	5	8	6	2
		Italy*	7	11	8	3
		Switzerland*	4	4	-	-
		Bulgaria	1	-	1	-
		Spain	1	1	1	-
		Germany*	5	5	1	1
		Finland	2	1	2	2
		France*	1	1	-	-
		Norway	2	1	1	-
		Poland	1	-	1	-
		Scotland	2	2	2	1
	North America		**8**			
		USA*	7	6	4	4
		Canada*	1	1	1	-
	Australia		**5**	4	1	2
Taxon						
		Bird	14	13	7	2
		Mammal	15	11	8	5
		Reptile	2	1	1	1
		Arthropod	9	12	8	7
		Annelid	2	1	1	-
		Nematode	3	2	1	-
		Protozoan	2	4	4	1
Biotic Measure						
	Population & Community Descriptor					
		Abundance	11	13	5	2
		Biomass	2	1	1	-
		Density	9	7	7	3
		Diversity	4	3	3	1
		Richness	11	7	6	1
		Dominant Species	3	4	5	4
	Population Viability Measure					
		Breeding Success	1	1	1	-
		Number of Nests	1	-	-	1
		Distance Travelled	5	3	2	-
		Recruitment	1	1	-	-
		Survival	4	1	3	2
		Frequency of Abandonment	1	1	-	-
	Fitness Measure					
		Body Condition	1	1	-	-
		Parasite Load	1	-	1	-
		Sprint Speed	1	1	-	-
		Stress Hormone	3	3	-	-
	Other Measure					
		Habitat Use	3	3	2	1
		Frequency of Occurrence	1	1	-	1
		Predicted Presence	1	1	-	-
Impact Type						
		Ski Run	22	26	21	11
		Resort Infrastructure	10	8	6	4
		Winter Tourism	9	8	2	0

*indicates a country with a major ski market [38]. 'Total' refers to the total number of published studies. 'Positive', 'No Effect' and 'Negative' refer to the specific effect(s) reported in each study. Note that the total number of specific effects may not equal the total number of studies, as individual articles may have reported more than one effect (e.g. an effect for each individual species, functional group, biotic measure etc. studied).

Taxonomic Groups

Just over one third of all studies investigated the impacts of ski infrastructure on mammals, with birds and arthropods also well represented in the literature. A smaller number of studies investigated other taxa. No studies focused on amphibians (Figure 4).

Regionally, there was variation in the taxonomic focus. Studies conducted in Europe investigated a diversity of taxonomic groups but the majority concentrated on birds and arthropods. In contrast, North American and Australian studies predominantly investigated mammals. Birds, reptiles and invertebrates were infrequently (or not) studied in these two regions (Figure 4).

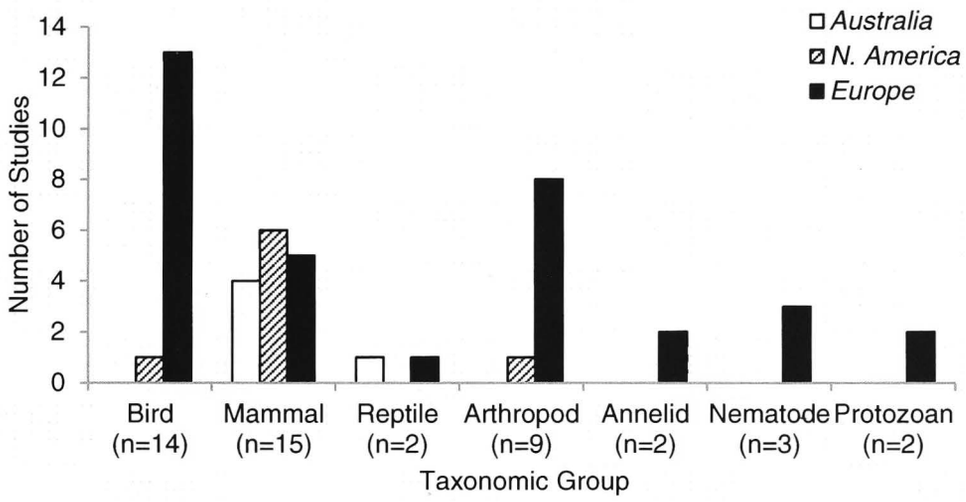

Figure 4. Number of studies (n = 41) investigating the impacts of winter recreation on different taxa across three continents. Four studies investigated multiple taxa, hence totals for taxonomic groups do not sum to the total number of studies analysed.

Effects of Winter Recreation

More than half the studies reported overall negative effects of human-generated disturbance on fauna in alpine and subalpine areas ($P < 0.001$). Few studies reported overall positive effects (Figure 5). The remainder reported overall non-significant ('no effect') or variable effects (i.e. a combination of positive, negative and non-significant effects dependent upon species or measure taken). For three reported measures (richness, diversity and abundance), sufficient information was provided to conduct a meta-analysis. This analysis confirmed the significant

negative impact that winter recreation has on the richness (d = -0.60, df = 7, 95% C.I.: -1.08 to -1.02; Figure 6) and diversity (d = -0.29, df = 5, 95% C.I.: -0.52 to -0.07; Figure 6) of alpine-subalpine fauna. Winter recreation also has a negative effect on the abundance (d = -0.23, df = 6, 95% C.I.: -0.70 to 0.25; Figure 6) of fauna, however this result was not significant.

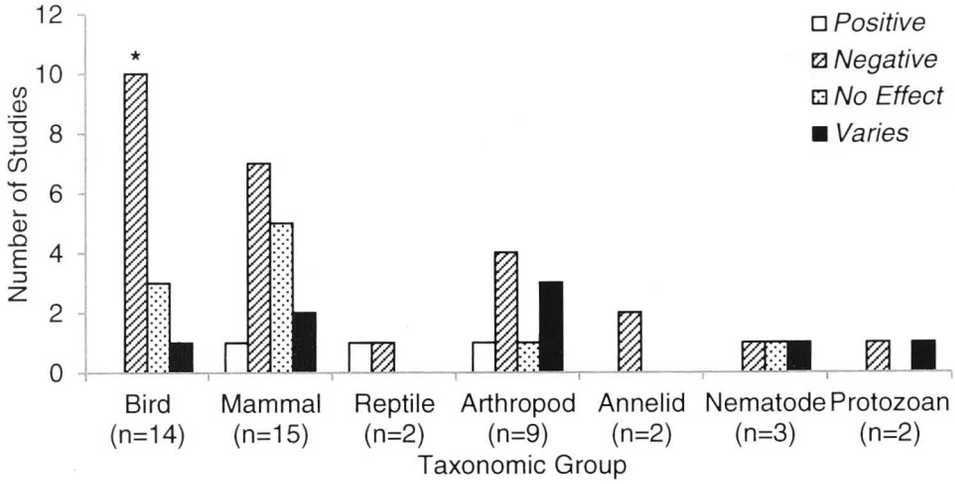

Figure 5. Number of studies (n = 41) investigating the effects of winter recreation on seven different taxonomic groups. **P < 0.01 indicates a significant difference between the number of positive and negative effects reported.

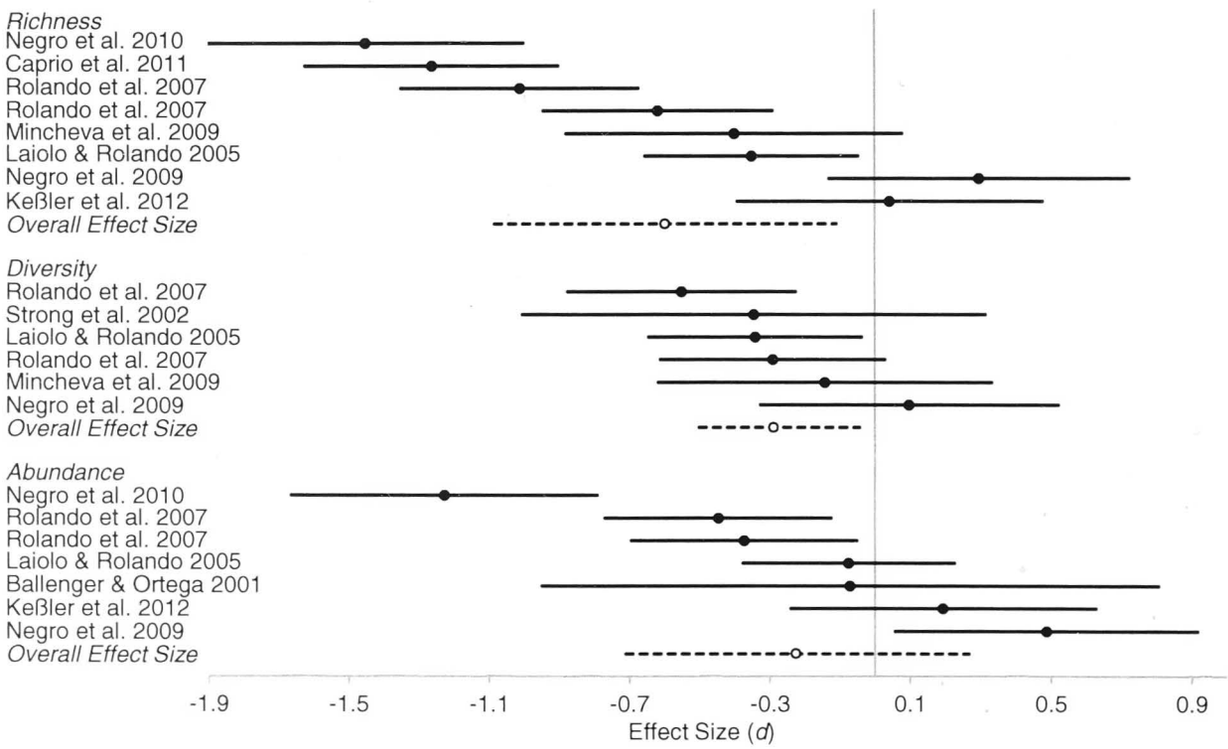

Figure 6. Overall and individual study effect sizes (± 95% C.I.) of winter recreation on fauna (d). Weighted effect sizes were calculated for meta-analyses on measures of richness, diversity and abundance.

When we analysed the effects of winter recreation by taxonomic group, we found that studies generally reported negative effects for winter recreation-related disturbances on birds ($P = 0.002$) and annelids; negative or variable effects on arthropods; and negative ($P = 0.07$) or non-significant effects on mammals. The results reported for reptiles, nematodes and protozoans were variable and did not show consistent trend patterns (Figure 5).

We also quantified how winter recreation affected biotic responses of different taxonomic groups. From 20 measures of biotic response reported across 41 studies, we pooled similar measures to collapse our data into four composite categories. These categories were: 1) population and community descriptors; 2) population viability measures; 3) fitness measures; and 4) other measures.

When composite categories were considered for each taxonomic group, protozoan ($n = 5$), nematode ($n = 2$), reptile ($n = 2$) and annelid ($n = 1$) sample sizes were too small for meaningful analysis. For all other taxonomic groups, population and community descriptors were the most commonly reported measures (Table 2). Winter recreation was often reported to have a negative effect on population and community measures for birds ($P = 0.18$) and arthropods ($P = 0.30$), but these were not significant results. For mammals, the effects were almost equally likely to be positive or negative ($P = 0.73$). However, when composite categories were pooled, winter recreation was significantly more likely to have a negative impact on birds ($P = 0.004$). Negative impacts were also common for mammals and arthropods but these results were not significant ($P = 0.29$ and $P = 0.21$ respectively; Table 2).

Regionally we found that, of the continents where the effects of skiing and resort infrastructure were investigated, European studies were more likely to report negative impacts of human-generated disturbance on fauna ($P < 0.001$), as were Australian studies (Figure 7). However, data from Australian studies were too sparse for statistical analysis. North American studies reported a range of effects but, again, data was too limited for statistical analysis.

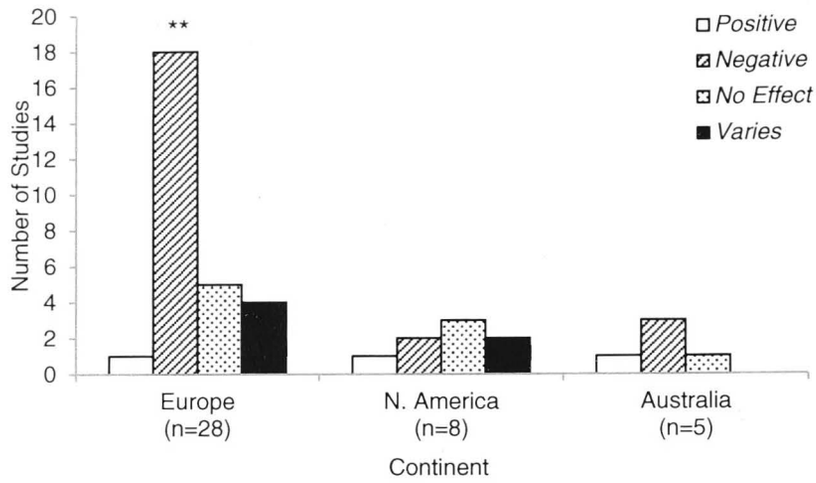

Figure 7. Number of studies (n = 41) investigating the effects of winter recreation on fauna across three continents. **P < 0.01 indicates a significant difference between the number of positive and negative effects reported.

We also considered how biotic responses to winter recreation varied by region. European studies primarily reported population and community measures, while Australian studies predominantly reported population viability measures. North American studies reported these measures evenly (Table 2). When composite categories were pooled for each region, disturbances were significantly more likely to be negative in Europe ($P < 0.001$). The effects of disturbance were also often reported to be negative in North America, but this trend was not significant ($P = 0.344$). In contrast, Australian studies reported positive effects almost as often as negative effects ($P = 0.687$; Table 2).

Finally, we analysed the effects of specific winter recreation-related disturbances on wildlife. We found that the effects of ski runs on fauna were well represented in the literature, while the effects of resort infrastructure and winter tourism were less frequently studied (Figure 8). Both ski runs and winter tourism were significantly more likely to have a negative impact on fauna ($P = 0.020$ and $P = 0.004$ respectively; Table 2). Resort infrastructure also had a predominantly negative effect, but this was not significant ($P = 0.388$; Table 2).

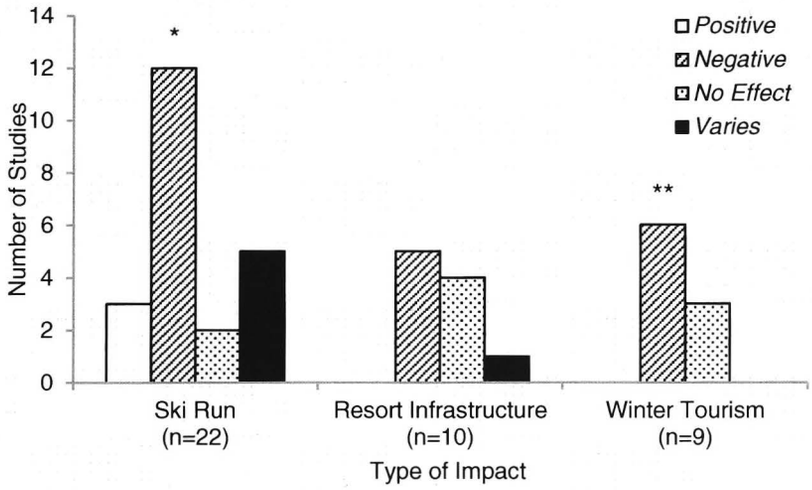

Figure 8. Number of studies (n = 41) investigating the effect of three different types of winter recreation-related disturbance on fauna. *P < 0.05, **P < 0.01 indicate a significant difference between the number of positive and negative effects reported.

Discussion

The negative impacts of winter recreation on fauna have often been highlighted in the alpine-subalpine literature [39,40,41,42]. However this article is the first systematic study of that literature. We addressed three key questions with respect to ski developments and impacts, and from these questions found that disturbances arising from winter recreation are more likely to have negative or non-significant impacts than have positive impacts on wildlife, regardless of taxonomic group, geographical region or specific type of ski modification. But more empirical studies are urgently required as many countries and taxa that are impacted by ski resorts are inadequately represented in the peer-reviewed literature.

The notion that ski resorts and their associated disturbances are likely to have negative impacts on biodiversity in alpine and subalpine areas is not surprising, as the construction of resort infrastructure requires the removal and modification of vegetation, as well as significant fragmentation of habitat over a small area [6]. While habitat fragmentation can have a variety of impacts on fauna [43], it is likely that habitat removal has the greatest effect on species with specialised habitat requirements [6]. This is particularly relevant to alpine-subalpine endemics of conservation concern such as the Mountain Pygmy Possum, *Burramys parvus*, in Australia and Raetzer's Ringlet, *Erebia christi*, in Europe [29].

However, for many species and taxa there is little or no information available in regards to the impacts of ski resorts and winter tourism. The negative effects of disturbances arising from winter recreation (such as decreased species richness or increased levels of stress hormones) were most frequently reported for mammals, birds and arthropods. These taxonomic groups are relatively well studied in the available literature and some species (and groups) have even been suggested as suitable bioindicators for alpine and subalpine ecosystems, such as the Black Grouse (*Tetrao tetrix*; [44,45]), syrphid flies [14,46] and grasshoppers [33,47]. As the impact of skiing is more likely to be negative on these prospective bioindicators, there is the potential that the effects of the ski industry are more extensive in alpine and subalpine environments than has been documented to date. This is because bioindicators tend to possess a moderate tolerance to disturbance, so it is likely that rare or sensitive species will already have been negatively affected by human-generated habitat modifications before the bioindicators show a response [48]. In addition, as many taxa remain poorly studied in areas affected by ski resorts, the suitability of bioindicators in representing general responses of fauna to disturbance in alpine-subalpine ecosystems cannot be adequately tested, nor can the lack of a response by a bioindicator be taken to mean that the community is not being adversely affected. Thus, more research is needed to improve our understanding of community interactions and species-level responses to disturbances in these environments.

We also need to improve our regional understanding of the impacts of winter recreation on wildlife. Most studies about the impacts of ski resorts on fauna come from Europe, with a smaller number of contributions from North America and Australia. Given that there are around 6000 ski areas located in more than 70 countries across the globe [38], many alpine and subalpine faunal communities around the world have not been studied. Thus, there is no regionally-relevant information about the effects of winter recreation on wildlife in many parts of the world. This is a concern as some countries with medium-sized developments (i.e. ski areas with 10 or more ski lifts) or large ski developments (i.e. ski areas with one or more major resorts) such as Andorra, New Zealand, Japan, China and Argentina [38] have not been the

focus of any empirical research published in the peer-reviewed literature. Yet, three of these countries have been listed as global biodiversity hotspots (New Zealand, Japan and China; [49]). In addition, according to the IUCN red list, many of these nations contain species of conservation concern in ski resort areas [29].

Finally, we must recognise that all types of winter recreation-related disturbance are more likely to have negative than positive impacts on fauna (particularly ski runs and winter tourism). However, investigations into the effects of resort infrastructure and winter tourism still need more attention, as published studies are uncommon. Identifying the effects of specific winter recreation-related disturbances is important as it will help to target management strategies for ski resorts. For example, if direct human provocation of fauna during winter has a negative effect on the fitness of individuals or populations, then an effective management strategy would involve the reduced access of tourists to areas where nests, dens or hibernacula are located. Other strategies such as modifying grooming techniques or reducing the extent of artificial snowing may not significantly improve the fitness levels of target populations. Thus, to improve conservation outcomes of fauna through targeted management strategies, more empirical studies are urgently needed.

Implications for Biodiversity Conservation

There has been an almost exponential increase in the number of scientific articles published investigating the impacts of winter recreation on fauna since the 1970s. However, at the same time the ski industry has seen a long period of expansion and consolidation [15]. For example, Japan has opened more than 450 new ski fields across the country since 1970, averaging more than 100 new ski fields per decade [50]. Therefore, while the increase in publications is positive for biodiversity conservation in alpine and subalpine areas, it is likely that ecological research has not kept pace with the expansion of the ski industry.

Our systematic review and meta-analysis indicates that significant knowledge gaps remain about the impacts of winter recreation on fauna. Globally, ski resorts are being managed with little empirical evidence (only 27 studies provide specific management actions), thus limiting the implementation of ecologically-sound practices (e.g. minimising damage to native vegetation [11]). There are indications that winter recreation is likely to have a negative impact but the available information is far from conclusive. Less intensively studied taxa and countries show inconsistent effects, and the impacts of ski resorts in unstudied regions and on unstudied taxa remain unknown. Thus there is an urgent need for more regional research if biodiversity is to be effectively conserved, as we cannot confidently assume that the effects reported in one set of regional studies (even on the same taxa) will apply elsewhere.

To best direct the research conducted in alpine and subalpine areas, we need to determine what we want from ecosystems. If the aim is to preserve the original community structure of fauna inhabiting areas impacted by ski tourism, we must rethink what we measure. Community composition and dominant species are often altered by disturbances arising from winter recreation [12,46,51] and specialist species are sometimes lost, despite "unchanged" overall species richness [14,46,52]. Yet, measures like species richness and abundance are the most commonly reported biotic measures (17/41 studies). Reporting measures of richness and abundance may improve study comparability. But to better understand disturbed communities in relation to reference communities, it would be more useful if measures of community composition and species dominance are also recorded [14].

It is also essential that the research in alpine-subalpine ecosystems consider long-term impacts (effects over greater than 10 years; [53]) of ski resorts on fauna. This is because alpine and subalpine vegetation regenerates slowly due to restricted growing seasons [54,55], so the effects of winter recreation-related disturbances like ski-run construction may take decades to begin to reverse [33,42,56,57]. However, long-term ecological studies are rare (only five studies

investigated the effects of development over more than 10 years), thus our knowledge of the cumulative effects of development and the efficacy of management actions is limited.

Caveats

We present a review of the global, peer-reviewed literature available to date. However, care needs to be taken when drawing conclusions from the results presented for several reasons. Firstly, "grey" literature was not included in this review due to the difficulty in obtaining this literature in a consistent and balanced way. Without the grey literature, areas identified as knowledge gaps, and regions identified as lacking in research output, may be overemphasized. That said, this highlights the fact that all research needs to be published via widely accessible avenues so that current research and management recommendations are available for use by all researchers, practitioners and government bodies.

A second caveat is that the small number of peer-reviewed papers available, the variability in methodologies, taxa studied and inconsistencies in reporting specific measures, precluded a more comprehensive meta-analysis. Thirdly, binomial tests were used to analyse the available data but due to the limited sample sizes, statistical significance could not always be reliably assessed, hence true effects occurring may not be emphasized.

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Supporting Information

Checklist S1. **PRISMA Checklist.**

Section/topic	#	Checklist item	Reported on page #
TITLE			
Title	1	Identify the report as a systematic review, meta-analysis, or both.	1
ABSTRACT			
Structured summary	2	Provide a structured summary including, as applicable: background; objectives; data sources; study eligibility criteria, participants, and interventions; study appraisal and synthesis methods; results; limitations; conclusions and implications of key findings; systematic review registration number.	2
INTRODUCTION			
Rationale	3	Describe the rationale for the review in the context of what is already known.	2-3
Objectives	4	Provide an explicit statement of questions being addressed with reference to participants, interventions, comparisons, outcomes, and study design (PICOS).	3
METHODS			
Protocol and registration	5	Indicate if a review protocol exists, if and where it can be accessed (e.g., Web address), and, if available, provide registration information including registration number.	n/a
Eligibility criteria	6	Specify study characteristics (e.g., PICOS, length of follow-up) and report characteristics (e.g., years considered, language, publication status) used as criteria for eligibility, giving rationale.	4-5
Information sources	7	Describe all information sources (e.g., databases with dates of coverage, contact with study authors to identify additional studies) in the search and date last searched.	4
Search	8	Present full electronic search strategy for at least one database, including any limits used, such that it could be repeated.	4
Study selection	9	State the process for selecting studies (i.e., screening, eligibility, included in systematic review, and, if applicable, included in the meta-analysis).	4-5, 7
Data collection process	10	Describe method of data extraction from reports (e.g., piloted forms, independently, in duplicate) and any processes for obtaining and confirming data from investigators.	5
Data items	11	List and define all variables for which data were sought (e.g., PICOS, funding sources) and any assumptions and simplifications made.	5-6
Risk of bias in individual studies	12	Describe methods used for assessing risk of bias of individual studies (including specification of whether this was done at the study or outcome level), and how this information is to be used in any data synthesis.	n/a
Summary measures	13	State the principal summary measures (e.g., risk ratio, difference in means).	6, 7
Synthesis of results	14	Describe the methods of handling data and combining results of studies, if done, including measures of consistency (e.g., I^2) for each meta-analysis.	6, 7

Section/topic	#	Checklist item	Reported on page #
Risk of bias across studies	15	Specify any assessment of risk of bias that may affect the cumulative evidence (e.g., publication bias, selective reporting within studies).	n/a
Additional analyses	16	Describe methods of additional analyses (e.g., sensitivity or subgroup analyses, meta-regression), if done, indicating which were pre-specified.	n/a
RESULTS			
Study selection	17	Give numbers of studies screened, assessed for eligibility, and included in the review, with reasons for exclusions at each stage, ideally with a flow diagram.	5, 7, Fig 2
Study characteristics	18	For each study, present characteristics for which data were extracted (e.g., study size, PICOS, follow-up period) and provide the citations.	5, Table S1
Risk of bias within studies	19	Present data on risk of bias of each study and, if available, any outcome level assessment (see item 12).	n/a
Results of individual studies	20	For all outcomes considered (benefits or harms), present, for each study: (a) simple summary data for each intervention group (b) effect estimates and confidence intervals, ideally with a forest plot.	6-9, Fig 3-8, Table 1
Synthesis of results	21	Present results of each meta-analysis done, including confidence intervals and measures of consistency.	9, Fig 6
Risk of bias across studies	22	Present results of any assessment of risk of bias across studies (see Item 15).	n/a
Additional analysis	23	Give results of additional analyses, if done (e.g., sensitivity or subgroup analyses, meta-regression [see Item 16]).	n/a
DISCUSSION			
Summary of evidence	24	Summarize the main findings including the strength of evidence for each main outcome; consider their relevance to key groups (e.g., healthcare providers, users, and policy makers).	10-11
Limitations	25	Discuss limitations at study and outcome level (e.g., risk of bias), and at review-level (e.g., incomplete retrieval of identified research, reporting bias).	13
Conclusions	26	Provide a general interpretation of the results in the context of other evidence, and implications for future research.	11-13
FUNDING			
Funding	27	Describe sources of funding for the systematic review and other support (e.g., supply of data); role of funders for the systematic review.	13

From: Moher D, Liberati A, Tetzlaff J, Altman DG, The PRISMA Group (2009). Preferred Reporting Items for Systematic Reviews and Meta-Analyses: The PRISMA Statement. PLoS Med 6(6): e1000097. doi:10.1371/journal.pmed1000097

For more information, visit: **www.prisma-statement.org**.

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* indicates studies included in the meta-analyses.

Table S1. **Systematic Review and Meta-analysis Proforma.**

Datum to be Extracted	Description of datum
Author(s)	*List the authors included on the publication*
Journal	*Name of journal article was published in*
Year Published	*Year of article publication*
Year(s) Studied	*Year(s) actual investigation was carried out*
Time to Publish	*Time taken for study to be published (numbers of years between last year of data collection to year of publication)*
Location(s)	*List the specific location(s) where the study was carried out*
Country	*List the specific country (or countries) where the study was carried out*
Continent	*Identify the continent where study was carried out*
Species or Community?	*Was a specific species studied or a faunal community? S/C*
Number of Species Studied	*How many species were studied?*
Species Studied	*List all the species studied (where possible)*
Taxonomic Group(s)	*List the broader taxonomic group(s) studied*
Justification for Study	*Identify the justification for the study where possible (brief)*
Specific Ski-Related Disturbance	*List the specific ski-related disturbances studied where possible (e.g. vegetation removal, use of artificial snow etc.)*
General Ski Infrastructure	*Classify and list the specific ski-related disturbances studied as related to "Ski Runs", "Resort Infrastructure" and/or "Winter Tourism/Human Disturbance"*
Study Quality	*Modified from* Felton et al. (2010)* *and* Pullin & Knight (2003)**. *Studies were assigned to one of four categories of quality:* *I. A controlled trial with matched pairs of treatments and controls. Scale of replication is suitable for subject taxa.* *II. Unpaired treatments and controls. Scale of replication is suitable for subject taxa.* *III. Unpaired treatments and controls. Scale of replication for study raises potential of confounding effects for subject taxa.* *IV. Inherent problems in methodology and/or experimental design.*
Biotic Measure(s) Reported	*List each of the biotic measures reported in the study*
Composite Category Reported	*Assign each biotic measure reported in the study to a composite category: Population and Community Measure, Population Viability Measure, Fitness Measure, or 'Other' Measure*
Statistic Provided (and/or significance level)?	*Is a statistic or significance level provided for any of the biotic measures reported? Y/N (Record the data and significance level where possible)*
Overall Effect Concluded	*Identify the overall effect of the ski-related disturbance on fauna (as concluded by the authors): Positive, Negative, No Effect or Varies (i.e. multiple effects concluded)*
Specific Effects Recorded	*Identify the specific effect (Positive, Negative or No Effect) recorded for each biotic measure reported in the study*
Specific Management Action Provided?	*Is a specific management action identified by the authors? Y/N*

*Felton A, Knight E, Wood J, Zammit C, Lindenmayer D (2010) A meta-analysis of fauna and flora species richness and abundance in plantations and pasture lands. Biol Conserv 143: 545-554.
**Pullin AS, Knight TM (2003) Support for decision making in conservation practice: An evidence-based approach. J Nat Conserv 11: 83-90.

Table S2. **Examples of positive, non-significant and negative effects for the four composite categories.**

Composite Category	Negative Effect	No Effect	Positive Effect
Population & Community Descriptors			
Abundance, Biomass and Density	Decrease in abundance, biomass or density in disturbed areas	No significant difference in abundance, biomass or density between disturbed and undisturbed areas	Increase in abundance, biomass or density in disturbed areas
Richness and Diversity	Decrease in richness, evenness or diversity in disturbed areas	No significant difference in richness, evenness or diversity between disturbed and undisturbed areas	Increase in richness, evenness or diversity in disturbed areas
Population Viability Measures			
Breeding Success	Decrease in breeding success in disturbed areas	No significant difference in breeding success between disturbed and undisturbed areas	Increase in breeding success in disturbed areas
Number of Nests	Decreased number of available nests in disturbed areas	No significant difference in number of available nests between disturbed and undisturbed areas	Increased number of available nests in disturbed areas
Survival	Decrease in survival rate in disturbed areas	No significant difference in survival rate between disturbed and undisturbed areas	Increase in survival rate in disturbed areas
Fitness Measures			
Body Condition	Decreased body condition in disturbed areas	No significant difference in body condition between disturbed and undisturbed areas	Increased body condition in disturbed areas
Parasite Load	Increased parasite load in disturbed areas	No significant difference in parasite load between disturbed and undisturbed areas	Decreased parasite load in disturbed areas
Sprint Speed	Increased sprint speed in disturbed areas	No significant difference in sprint speed between disturbed and undisturbed areas	Decreased sprint speed in disturbed areas
Stress Hormone	Increased stress hormone levels in disturbed areas	No significant difference in stress hormone levels between disturbed and undisturbed areas	Decreased stress hormone levels in disturbed areas
Other Measures			
Habitat Use	Decreased use of habitat in areas affected by ski resorts	No significant difference in habitat use inside and outside of areas affected by ski resorts	Increased use of habitat in areas affected by ski resorts
Frequency of Occurrence	Decreased frequency of occurrence in disturbed areas	No significant difference in frequency of occurrence between disturbed and undisturbed areas	Increased frequency of occurrence in disturbed areas

Examples of results we classified as 'negative', 'non-significant' (no effect) and 'positive' for biotic measures reported in the articles we included for review. Biotic measures (hence their reported effects) were subsequently sorted into four composite categories (population and community descriptors, population viability measures, fitness measures and other measures) for analysis.

Table S3. Comparison of the contribution of seven regions to the peer-reviewed literature investigating the impacts of ski-related disturbances on wildlife, compared with the proportion of all ski areas located in those seven regions (based on approximate numbers of ski areas provided by [38]).

Region	Proportion of studies	Proportion of all ski areas
Australia	0.12	0.002
New Zealand	0	0.005
Asia	0	0.21
South Africa	0	0.0002
South America	0	0.009
North America	0.20	0.16
Europe	0.68	0.62

Table S4. **Provision of management recommendations by region and time period.** "Y" indicates that a recommendation was provided; "N" indicates that a recommendation was not provided.

Year	Australia	North America	Europe
1970-1979	-	-	1Y
1980-1989	1Y	-	1Y, 2N
1990-1999	-	2Y	2N
2000-2009	3Y, 1N	3Y, 2N	10Y, 6N
2010-present	-	1Y	5Y, 1N

PAPER II: The Impacts of Ski Resorts on Reptiles: A Natural Experiment.

Globally, ski-related disturbances are more likely to have negative effects than positive effects on alpine and subalpine fauna. However, limited research is available regarding the effects of ski resorts on reptiles. This lack of research raises concerns about the type and extent of impacts ski resorts have on the occurrence and persistence of reptiles, and the effectiveness of management strategies (if any) in mitigating adverse impacts. In this paper, I quantify the effects of ski-related disturbances on reptiles using a natural experiment.

Sato, C.F., Wood, J.T., Schroder, M., Green, K., Michael, D.R. & Lindenmayer, D.B. (2013) The impacts of ski resorts on reptiles: A natural experiment. Animal Conservation. doi: 10.1111/acv.12095

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Abstract

Alpine-subalpine areas are sensitive environments that support large numbers of endemic species. They are also popular for human recreation. Increasing demands for tourism means that infrastructure in alpine resorts is expanding. Consequently, habitat is being modified and fragmented, potentially adversely affecting fauna. However, research investigating the effects of ski resorts on wildlife, particularly reptiles, is limited, and the effectiveness of management strategies in mitigating adverse impacts is unknown. To quantify the effects of ski-related disturbances on specialist and generalist reptile species, we surveyed sites in disturbed and undisturbed subalpine habitats. We also examined vegetation composition and habitat structure to determine whether structural or compositional habitat features were driving patterns of reptile occurrence. Our results indicate the effects of ski-related disturbance varied between species, but that adverse effects - particularly on ski runs - were more pronounced for specialists. Given that each species studied was positively associated with compositional or structural features of the environment, we argue that alterations to these habitat attributes when creating ski runs will supress lizard abundances in these areas. However, while ski runs have an adverse effect on reptiles, the persistence of these animals in ski resorts can be facilitated by retaining habitat structure, and minimising disturbance to native vegetation.

Keywords: *habitat structure; lizard; ski run; specialist; subalpine; vegetation composition*

Introduction

Alpine and subalpine areas attract tourists year-round for their scenic beauty (Messerli, 1987), unique wildlife (Nagy & Grabherr, 2009) and winter recreation (Pickering *et al.*, 2003). Winter tourism contributes significantly to the GDP of many countries (UNEP, 2007). Hence, it is in those countries' interest to continue developing alpine-subalpine areas to meet the demands of patrons. Consequently, these environments are subject to habitat loss and fragmentation (WWF, 2005), two processes that have negative effects on fauna (Lindenmayer & Fischer, 2006).

Adverse impacts of ski-related disturbances on alpine-subalpine ecosystems are concerning as these environments are species-rich and support many endemic taxa (Körner, 2004; Martin, 2013). Significant losses of biodiversity could therefore occur in these areas without the implementation of management plans informed by rigorous, empirical research. However, limited peer-reviewed research has investigated the effects of ski-related disturbances on wildlife (Sato, Wood & Lindenmayer, 2013a). The published research indicates that ski disturbances have predominantly negative effects on fauna, reducing the abundance, diversity and richness of birds, arthropods and mammals (Sato *et al.*, 2013a). However, for reptiles, the impacts of ski resorts remain unclear as conclusions from the two published studies are inconsistent (Sato *et al.*, 2013a).

In non-alpine ecosystems, disturbances such as habitat fragmentation have varying effects on reptiles. Fragmentation can be beneficial because it alters thermal environments, offering reptiles more thermoregulatory opportunities (Rubio & Simonetti, 2011; Vitt *et al.*, 1998). It may also increase landscape heterogeneity, providing a variety of environmental conditions that can support the needs of a greater diversity of species (Fischer *et al.*, 2005). However, clear-cutting vegetation generally makes landscapes less habitable for reptiles [e.g. in forests (D'Cruze & Kumar, 2010), agricultural areas (Driscoll, 2004) and plantations (Fischer *et al.*, 2005)].

Vegetation and rock removal is undertaken during the initial construction of ski runs, through grooming, rock blasting and rehabilitation of slopes with exotic grasses (Ries, 1996; Tsuyuzaki, 1994). Seasonal maintenance practices (e.g. mowing) then prevent the re-establishment of woody vegetation (PBPL, 2002). Both the initial construction and ongoing management of ski runs is undertaken to improve snow condition and skier safety (Kelsall & Finch, 1996). However, these activities result in the simplification of habitat structural complexity (e.g. removal of rocks and logs) and the alteration of vegetation composition, two important drivers of reptile richness and abundance in non-alpine environments (Martin & Murray, 2011; Michael, Cunningham & Lindenmayer, 2008). Thus, it is likely that ski-related disturbances, and the resulting loss of these important habitat components that are used for basking, and sheltering, will negatively affect reptiles in subalpine areas.

Given the documented trend of the loss of specialist taxa following anthropogenic disturbance [e.g. birds (Devictor *et al.*, 2008) and lepidopterans (Ekroos, Heliola & Kuussaari, 2010)], it is likely that specialist reptile species in subalpine environments will be more sensitive than generalists to the modification of vegetation composition and simplification of habitat structure (McKinney, 1997; Preston, 1962; but see Attum *et al.*, 2006). Because alpine areas cover only a small proportion of the Earth's terrestrial landmass (*c.* 7.9%, Körner, Paulsen & Spehn, 2011) and sensitivity to disturbance has been documented previously for specialist reptile species (Foufopoulos & Ives, 1999; Sarre, Smith & Meyers, 1995), further disturbance to alpine-subalpine ecosystems from ski resort development could result in the permanent loss of specialised reptile taxa from these environments.

In this study, we used a natural experiment to quantify the effects of ski-related disturbances on reptiles. Specifically, we asked the following key questions: (1) Do ski-related disturbances affect the abundances of reptiles? (2) Are the patterns of reptile distribution driven by structural

or compositional habitat features? (3) Are the effects of ski-related disturbances more pronounced for specialist species?

First, we postulated that ski resorts would have a negative effect on reptile abundance, principally in areas where intensive clearing of vegetation has occurred (e.g. on ski runs). This is consistent with the negative effects of ski runs observed for other taxa in alpine-subalpine areas (Sato *et al.*, 2013a), and with the negative effects of intensive vegetation removal on reptiles (e.g. Driscoll, 2004; D'Cruze & Kumar, 2011). Second, we postulated that the observed patterns would be driven by modifications to vegetation composition and/or simplifications to habitat structure, given the documented importance of these habitat attributes to reptiles (Michael *et al.*, 2008; Martin & Murray, 2011). Finally, we postulated that in areas subject to substantial alteration of vegetation cover and structure, the negative effects of disturbance on the abundance of reptiles will be more pronounced for specialist species than for generalists. This is because specialists have a narrower niche than generalists, thus are less tolerant of disturbances that limit the availability of resources upon which they rely (Levins, 1968).

The results of our study provide much needed information about the ecology and conservation of subalpine reptiles. Based on these important new insights, we propose measures to mitigate potential negative effects of habitat modification on reptile assemblages occurring in and around ski resorts. This has implications for the management of ski areas worldwide, many of which currently do not address the needs of reptiles in their management strategies (e.g. PBPL, 2002; RMOW, 2007).

Methods

Study Species

We characterised the four reptile species in our study as specialists or generalists based on the breadth of their ecological requirements (see Supporting Information Table S1).

Cyclodomorphus praealtus (alpine she-oak skink), *Liopholis guthega* (Guthega skink), and *Pseudemoia pagenstecheri* (grassland tussock skink) are specialist reptiles, whereas *Pseudemoia entrecasteauxii* (woodland tussock skink) is a generalist reptile (Supporting Information Table S1). All the species occur in the Australian Alps (Green & Osborne, 2012), but two (*C. praealtus* and *L. guthega)* are rare and restricted to elevations above 1500 m (Green & Osborne, 2012). The *Pseudemoia* species have a wider distribution across south-eastern Australia (Wilson & Swan, 2008). Invertebrates are assumed to comprise a large proportion of the diet for all four species (Green & Osborne, 2012) but vegetation may be consumed opportunistically (Brown, 1991). *Liopholis guthega* is the only species that appears to have specific shelter-site requirements, constructing burrow networks under large granitic boulders which may be shared by large colonies of individuals (Michael & Lindenmayer, 2010).

Study Area

We conducted our study in Kosciuszko National Park, south-eastern Australia (Fig. 1a). We surveyed reptiles at two ski resorts: Perisher (36°24'S 148°24'E) - comprising Guthega, Smiggin Holes and Perisher ski centres - and Charlotte Pass (36°26'S 148°20'E; Fig. 1), located between 1640-2050 m. The study area is characterised by Snow Gum (*Eucalyptus niphophila*) woodlands, wet heathlands (*Epacris* spp., *Baeckea utilis*) and dry heathlands (*Kunzea muelleri*, *Nematolepis ovatifolium*, *Prostanthera cuneata*), sod tussock grasslands (predominantly *Poa costiniana* and *Rytidosperma nudiflorum*), and bog communities (Costin *et al.*, 2000). The survey areas within the ski resorts are characterised by disturbed grasslands (*Agrostis capillaris*, *Festuca rubra*). Mid-summer temperatures average 10 °C, while winter temperatures are frequently below freezing (Costin *et al.*, 2000). Annual precipitation is greater than 2000 mm per year, with summers drier than winters (Green & Osborne, 2012). The study area is snow covered typically from mid-June to October.

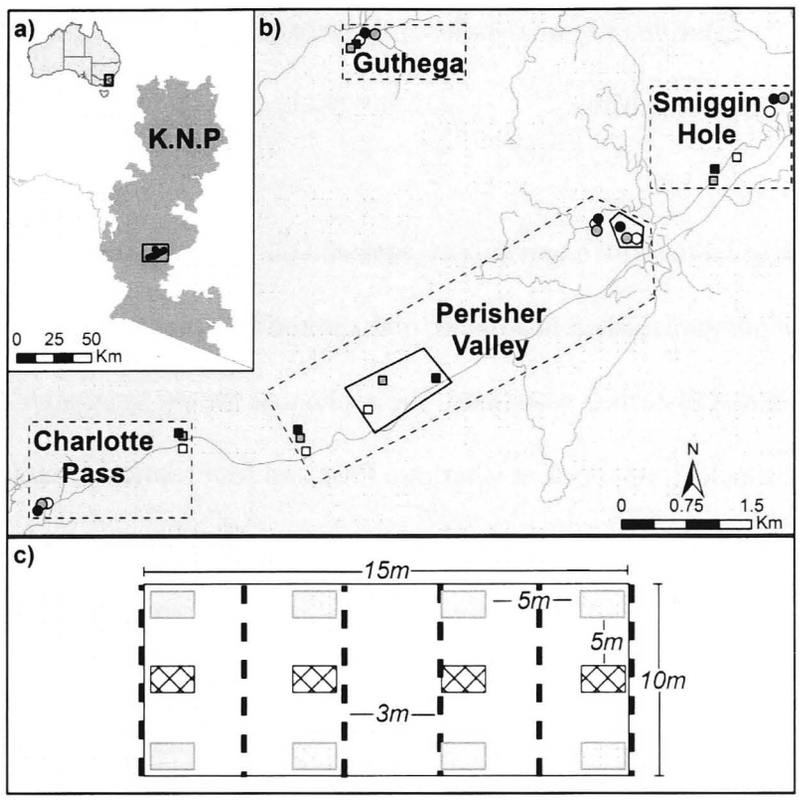

Figure 1. Study Area and Site Maps. a) The study area in Kosciuszko National Park, south-eastern Australia. b) Location of the replicate 'blocks' within Kosciuszko National Park. Dashed polygons represent each block. At Perisher Valley we established two blocks, thus the second block is differentiated by closed polygons. Within each polygon, circles represent disturbed sites and squares represent undisturbed sites. Shading of circles and squares indicates different habitat types i.e. white = grassland, grey = heathland, black = woodland. Grey lines indicate roads. c) Diagram of the trap layout used at each 10x15-m site. Crosshatched rectangles represent funnel traps and grey rectangles represent roof tiles. Thick, vertical dashed lines represent transects for vegetation surveys.

Experimental Design

We established a blocked experiment comprising three habitat types (grassland/heathland/woodland) in two disturbance categories (disturbed/undisturbed). We located the three disturbed habitat types within each ski resorts. We established disturbed grassland sites in the centre of wide (> 40 m), graded ski runs that had been cleared of vegetation, and rehabilitated with exotic grasses (predominantly *A. capillaris* and *F. rubra*) during initial construction. We positioned disturbed heathland sites alongside ski runs showing signs of slope grooming and vegetation slashing. We selected small, fragmented patches of woodland surrounded by ski runs as disturbed woodland sites. We located undisturbed examples of these habitat types outside the resorts in sod tussock grasslands, dry heathlands, or Snow

Gum woodlands that exhibited minimal signs of disturbance from ski resort development or natural processes such as wildfires.

We selected sites to enable a full experimental factorial design, yielding six 'treatments': undisturbed grassland, undisturbed heathland, undisturbed woodland, disturbed grassland, disturbed heathland and disturbed woodland. We replicated the six treatments five times in complete replicate blocks (one block at Charlotte Pass and four replicate blocks at Perisher), giving a total of 30 sites (Fig. 1b). All sites were 10 x 15-m rectangular plots located on south-facing slopes between 1600 and 1850 m a.s.l., separated from one another by at least 50 m to maximise the chances that observations of lizards in one site were independent from observations of lizards in nearby sites (given the limited dispersal capabilities of lizards; James, 1991; Clobert *et al.*, 1994).

Lizard Surveys

To maximise reptile detections, we surveyed lizards using three common survey techniques: cover objects (roof tiles), funnel traps and active searches (Michael *et al.*, 2012). Different species differ in their propensity to be detected using different survey techniques, therefore a variety of methods are required to produce robust estimates of abundance (Michael *et al.*, 2012).

During surveys, we placed eight concrete roof tiles (30 x 40 cm) at each site (Fig. 1c), then checked each tile once a day for four consecutive days, recording observations of any reptiles using tiles.

We also set four funnel traps (~75 x 18 x 18 cm; Terrestrial Ecosystems; Thompson & Thompson, 2007) on the first day of a survey period and left them open for three trap nights. We positioned the traps through the centre of a site (Fig. 1c), selecting locations likely to be utilised by lizards (e.g. alongside vegetation or rocks). In the trap, we placed an upturned plastic plate for shelter and a water-soaked sponge ('rehydrated' each day) to prevent the dehydration

of captured animals. For the three days following, we checked the traps, recorded captured individuals and released them at point of capture.

Additionally, we conducted non-destructive, time- and area-constrained (15min/150 m^2) active searches for each day of the 4-day survey period. We systematically moved through sites searching for reptiles around vegetation, rocks, logs and bark. We recorded all observations of reptiles seen during this period.

We surveyed a maximum of 10 sites during a 4-day period, thus we required three survey periods (i.e. 12 days) to visit all 30 sites. To avoid temporal bias in lizard numbers, we randomised the timing of visits to sites to ensure that we surveyed any given field site evenly during 'morning' [0830-1200 Australian Eastern Standard Time (AEST)] and 'afternoon' (1200-1530 AEST) sessions of a 4-day survey period. We completed three surveys (i.e. 12 days per site, 36 days total) during November-December 2010, January-February 2011 and November-December 2011.

Vegetation Sampling

We conducted vegetation surveys during April 2011, recording habitat features that are potentially important for lizards. At each site, we counted the number of logs (≥ 10 cm diameter), tree trunks (≥ 10 cm diameter) and rocks in three different size classes (< 2, 2-5, > 5 m^3). We also visually estimated the total volume of fine (< 6 mm diameter) and coarse (6-99 mm diameter) woody debris to the nearest 5%. Along six parallel 10-m transects separated from one another by 3 m (Fig. 1c), we used the point-intercept method (Goodall, 1952) to determine the percentage cover of native and exotic plant species, plant growth forms (grass/shrub/tree) and four substrates (bare ground, litter, rocks and logs) at 1-m intervals. At 2-m intervals, we measured vegetation height and visually estimated understorey vegetation density. We also estimated total vegetation cover above the ground (i.e. any vegetation from the canopy, understorey or ground strata contributing to cover above the camera; Fig. 2) from photographs

taken using a Canon EOS 500D digital camera fitted with an Opteka fish-eye lens (modified from Pringle, Webb & Shine, 2003).

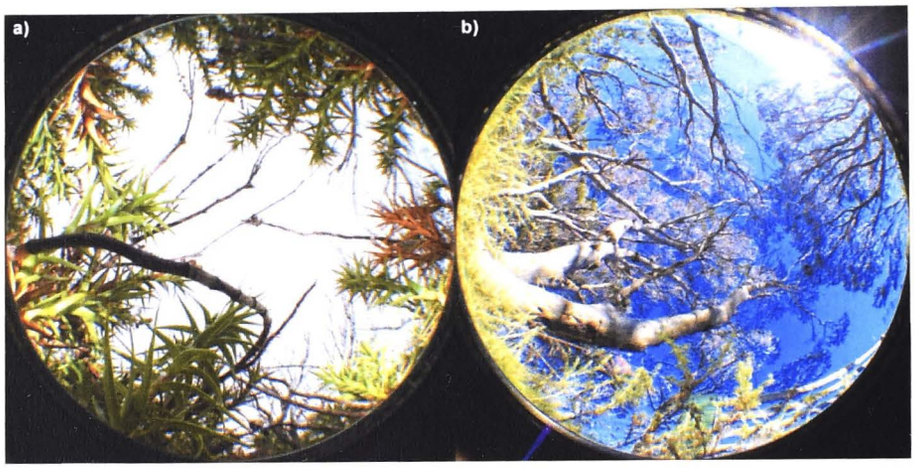

Figure 2. Representative hemispherical photographs for (a) heathland and (b) woodland from which we estimated total vegetation cover above the ground (i.e. ground cover vegetation (e.g. grasses), understorey vegetation (e.g. shrubs) and canopy cover vegetation (e.g. snow gum trees) that contributed to cover above the camera).

Statistical Analysis

In the initial stages of our analysis, we ignored the random structure of the data and fitted generalized linear models (GLMs) to identify six potentially influential habitat predictors for each lizard species (Supporting Information Table S2). This allowed us to remove highly correlated variables from further analyses and reduce the number of candidate variables (Supporting Information Table S2) included in the final models. We fitted a quasi-Poisson distribution with a log-link function to the response variable for each GLM. We selected the best model from all possible models for each lizard species, based on Akaike's Information Criterion (AIC; Akaike, 1973) and the biological relevance of the model. We include all models and AIC values in Supporting Information Table S2.

To explore the effect of broad- and fine-scale habitat variables on the abundance of lizard species, we fitted hierarchical generalized linear models (HGLM; Lee, Nelder and Pawitan, 2006) for common species (*P. entrecasteauxii* and *P. pagenstecheri*). Here we assumed a quasi-Poisson distribution with a log-link function for the response and a gamma distribution with a

log-link function for the random component. Due to the limited number of observations for *C. praealtus* and *L. guthega*, we only fitted log-linear models (GLM) for these two rare species.

For each species, we ran two sets of models. We focused the first set of models on broad-scale habitat type and presence/absence of disturbance (termed 'Site'). We focused the second set of models on the fine-scale habitat attributes we identified from our initial exploratory regressions. In all models, we included the total number of lizards observed per day as the response variable. For the HGLMs, we included 'Time', 'Block' and 'Site' as random effects to account for spatial and temporal correlations in the data. Additionally, if we did not detect a species in a broad habitat type (e.g. grassland, heathland or woodland), we excluded it from analysis for that species. We fitted all models using GenStat 16 (VSN International Ltd, Hertfordshire, UK).

We used canonical correspondence analysis (CCA; McCune & Grace, 2002) to determine the influence of dominant plant species abundance on the occurrence of individual lizard species. For our main matrix, we used presence/absence data for each lizard species at each site. We considered a species as being 'present' at a site if it was detected in at least one survey. For our secondary matrix, we selected dominant plant species across all sites if: (1) The species occurred in greater than two sites; and (2) The species had a mean percentage cover (across all sites it was present in) of greater than 9%. Using a cut-off of 9% ensured that we included species which were dominant at some sites (i.e. greater than 20% coverage at a site), but rare at others. Applying these constraints, we retained 18 plant species for our secondary matrix. We provide the 'dominant' plant species included in the CCA in Supporting Information Table S3. We used weighted average scores to construct our CCA axes. We assessed their significance (i.e. tested the hypothesis that there was no correlation between the primary (lizard species presence) and secondary (plant species abundance) matrices using Monte Carlo simulations. *P*-values were based on the proportion of 999 Monte Carlo simulations with an eigenvalue greater than our observed eigenvalue. We performed CCA using PC-ORD 5 (McCune & Mefford, 1999).

Results

Across the three survey periods, we recorded 950 lizard observations from four different species: *C. praealtus*, *L. guthega*, *P. entrecasteauxii* and *P. pagenstecheri*. We observed *C. praealtus* and *P. entrecasteauxii* in all habitat types, *L. guthega* in heathland and woodland only, and *P. pagenstecheri* in heathland and grassland only. Total numbers of each species observed in each habitat type are included in Table 1.

Table 1. Total abundances for four lizard species in each habitat type surveyed and for each survey method used. Abundances are pooled across three survey periods (Nov-Dec 2010, Jan-Feb 2011, Nov-Dec 2011). Habitat types are indicated by DG (disturbed grassland), UG (undisturbed grassland), DH (disturbed heathland), UH (undisturbed heathland), DW (disturbed woodland), UW (undisturbed woodland). Survey methods are indicated by T (Tile), FT (Funnel Trap) and AS (Active Searching).

Species	Survey Method	DG	UG	DH	UH	DW	UW	Total
Cyclodomorphus praealtus	T	4	22	4	6	1	3	40
	FT	0	5	1	3	0	0	9
	AS	0	2	0	2	1	0	5
	Total	*4*	*29*	*5*	*11*	*2*	*3*	*54*
Liopholis guthega	T	0	0	3	3	0	0	6
	FT	0	0	1	11	0	4	16
	AS	0	0	5	42	3	34	84
	Total	*0*	*0*	*9*	*56*	*3*	*38*	*106*
Pseudemoia entrecasteauxii	T	1	6	12	2	10	6	37
	FT	2	4	4	2	3	4	19
	AS	14	66	76	65	171	157	549
	Total	*17*	*76*	*92*	*69*	*182*	*170*	*605*
Pseudemoia pagenstecheri	T	0	11	0	0	0	0	11
	FT	1	5	1	5	0	0	12
	AS	1	127	10	23	0	0	161
	Total	*2*	*143*	*11*	*28*	*0*	*0*	*184*

Broad-Scale Habitat Preferences

GLMs and HGLMs indicated that the abundances of each species differed significantly among habitat types (GLM: *C. praealtus*: F-statistic = 16.68, df = 5, $P < 0.001$, *L. guthega*: F-statistic = 11.87, df = 3, $P < 0.001$; HGLM: *P. entrecasteauxii*: $\chi^2_5 = 17.86$, $P = 0.003$, *P. pagenstecheri*: $\chi^2_3 = 28.30$, $P < 0.001$; Supporting Information Table S4). However, broad-scale habitat preferences varied between species. The only relationship common to all species was the strong negative association with, or absence from, disturbed grasslands.

Cyclodomorphus praealtus (rare specialist; Supporting Information Table S1) was most abundant in undisturbed grassland (Fig. 3a). Weak positive associations with heathlands and negative associations with woodlands were apparent but not significant (Fig. 3a; Supporting Information Table S4). *Liopholis guthega* (rare specialist; Supporting Information Table S1) was not detected in grasslands, was least abundant in disturbed areas (Fig. 3b), but was positively associated with undisturbed heathland and woodland (Supporting Information Table S4). *Pseudemoia entrecasteauxii* (common generalist; Supporting Information Table S1) was the most abundant species in all habitat types, exhibiting positive associations with all habitat types except disturbed grassland (Fig. 3c; Supporting Information Table S4). Finally, we recorded significantly more observations of *P. pagenstecheri* in undisturbed grasslands and heathlands, and significantly fewer observations in disturbed grasslands (Fig. 3d; Supporting Information Table S4). *Pseudemoia pagenstecheri* (common specialist; Supporting Information Table S1) was not detected in woodlands.

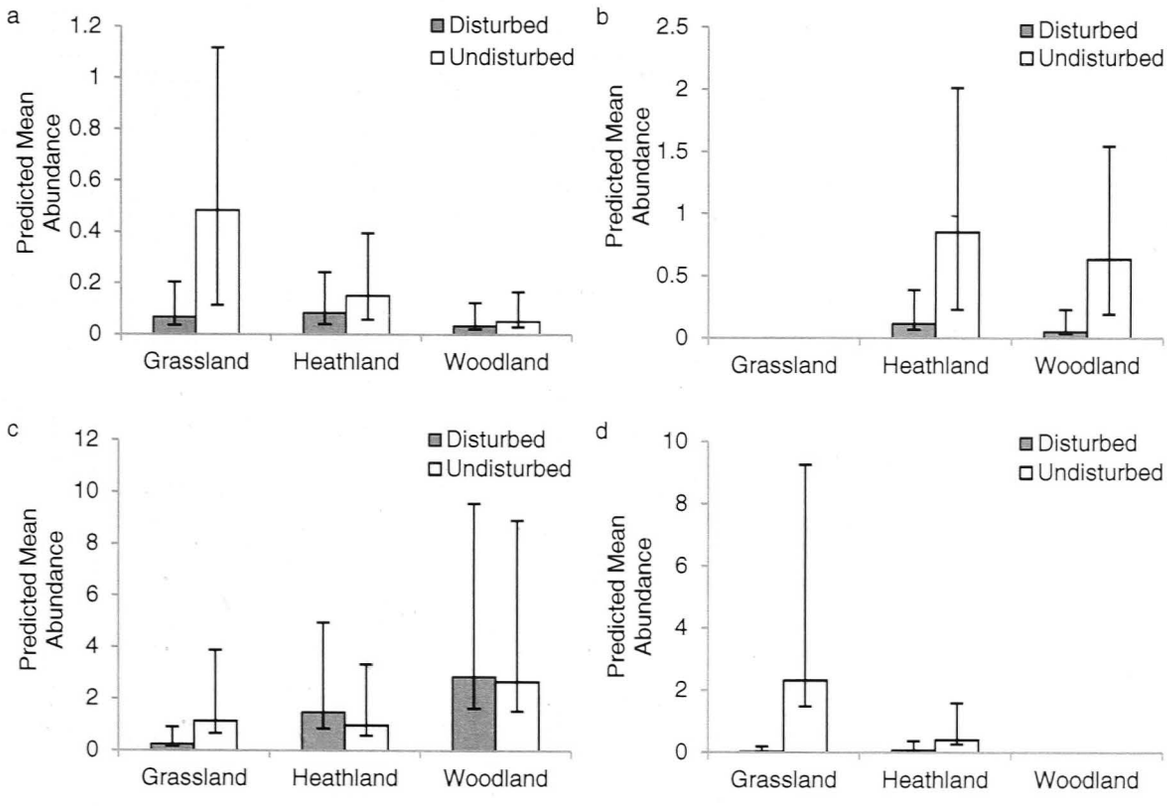

Figure 3. Predicted mean abundances (± 95% confidence interval) for four species of lizard (a) *Cyclodomorphus praealtus*, (b) *Liopholis guthega*, (c) *Pseudemoia entrecasteauxii*, (d) *Pseudemoia pagenstecheri*, in six habitat types: disturbed and undisturbed grasslands, heathlands and woodlands. We replicated the six habitat types at five blocks, and surveyed all sites on three separate occasions. All predicted abundances are given on the natural scale.

Fine-Scale Habitat Preferences

The results of HGLMs exploring fine-scale habitat associations of lizard species are shown in Table 2. *Cyclodomorphus praealtus* showed a significant, negative association with the number of logs on site and total vegetation cover, but a significant, positive association with native grass cover. *Liopholis guthega* showed significant, positive associations with the number of large rocks (> 5 m^3) on site and total vegetation cover, but significant, negative associations with leaf litter cover, ground layer density and native grass cover. *Pseudemoia entrecasteauxii* showed a significant, positive association with the volume of woody debris. Finally, *P. pagenstecheri* showed a significant, negative association with exotic grass cover and understorey shrub cover.

Table 2. Fine-scale habitat associations for four species of lizard based on HGLMs (for *P. entrecasteauxii* and *P. pagenstecheri*) and GLMs (for *C. praealtus* and *L. guthega*). Habitat features indicated by TL (number of logs), TVWD (volume of woody debris), R>5 (number of rocks greater than 5 m^3), USSC (% understorey shrub cover), TVC (% total vegetation cover), EGC (% exotic grass cover), LLC (% leaf litter cover) and GLD (% ground layer density). Blank cells indicate that a variable was not significant or not included in the model for that species. **P* < 0.05, ***P* < 0.01, ****P* < 0.001

	C. praealtus			*L. guthega*			*P. entrecasteauxii*			*P. pagenstecheri*		
	Estimate	SE	*P*	Estimate	SE	*P*	Estimate	SE	*P*	Estimate	SE	*P*
Intercept	-2.70	0.36		1.00	0.70		-0.06	0.22		0.77	0.36	
TL	-0.86	0.34	*									
TVWD							0.07	0.02	**			
R>5				0.41	0.06	***						
USSC										-0.04	0.01	***
TVC	-0.01	0.006	*	0.25	0.06	***						
EGC										-0.04	0.01	***
NGC	0.02	0.003	***	-0.02	0.01	***						
LLC				-0.09	0.02	***						
GLD				-0.17	0.05	***						

The CCA revealed a strong relationship between plant species abundance and the presence of lizard species, with the three axes of the CCA cumulatively explaining 78.5% of the variation observed in the dataset. The first axis of the CCA explained most of the variation (48%) and represented an increasing abundance of *P. cuneata* and *N. ovatifolium* (shrub species) at a site. The second axis explained 19.7% of the variation and represented a decreasing abundance of *E. niphophila* (tree species) and an increasing abundance of *Empodisma minus* (herb species). The

third axis explained 10.8% of the variation and represented a decreasing abundance of *Epacris glacialis* (a small shrub species).

Using the first two axes to explore lizard-plant species relationships (Fig. 4), we found that we were more likely to observe: (1) *C. praealtus* and *P. pagenstecheri* in habitats where *E. minus* (a characteristic herb species of sod-tussock grasslands; Costin *et al.*, 2000) was dominant; (2) *L. guthega* in habitats where *N. ovatifolium* and *P. cuneata* (characteristic shrub species of rocky heathlands; Costin *et al.*, 2000) were dominant; and (3) *P. entrecasteauxii* in habitats where *Olearia brevipedunculata*, *Olearia phlogopappa* (both shrub species) and *E. niphophila* (tree species) were dominant. The Monte Carlo test using 999 permutations found that the first two axes were significant ($P < 0.05$), indicating that the observed relationships were not random.

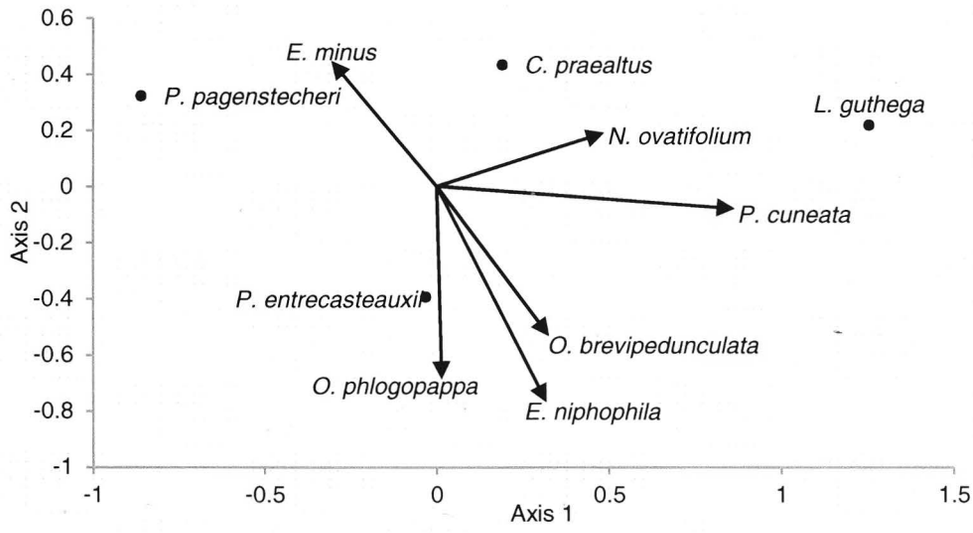

Figure 4. CCA ordination of lizard species and dominant plant species. Arrow length indicates the importance of a plant species in the model and its influence in explaining the patterns of lizard distribution (i.e. longer arrow = greater influence). The location of a species relative to arrows indicates the vegetation preferences of that species.

Discussion

We sought to quantify: (1) the effects of ski-run related disturbances on the abundance of reptiles; (2) whether reptile distributions are driven by structural or compositional habitat features; and (3) whether the effects of ski-related disturbances are more pronounced for

specialists than generalists. We found that the effects of ski-related disturbances varied between species, but that adverse effects - particularly on ski runs - were more pronounced for specialists (*C. praealtus*, *L. guthega* and *P. pagenstecheri*). Given that each of the lizards was positively associated with either compositional or structural habitat features, we argue that alteration to vegetation composition or structure when creating ski runs will supress lizard abundances in these areas.

Our findings indicated that lizards avoid ski runs in preference for more structurally complex habitat types (e.g. heathlands, woodlands and undisturbed grasslands). Like Amo, Lopez & Martin (2007), we argue that the extreme structural simplification of ski runs explains the low numbers of lizards in these areas. Without the cover of native vegetation, woody debris or rocks, ski runs offer reptiles limited shelter from predators (Amo *et al.*, 2007) and leaves them exposed to extreme thermal conditions (Sato *et al.*, 2013b), threatening their immediate and long-term survival in these areas. To encourage the use (and potential re-colonisation) of ski runs by reptiles, essential actions include reconnecting isolated habitats through the restoration of native vegetation and re-introduction of habitat features, such as semi-submerged rocks or timber.

The restoration of ski runs with native vegetation may have additional benefits for reptiles as native-dominated habitats support greater prey diversity (e.g. invertebrates) than exotic-dominated habitats (Valentine, Roberts & Schwarzkopf, 2007; Bateman & Ostoja, 2012). Indeed, invertebrate assemblages can be altered dramatically by vegetation alterations arising from ski run construction (Strong, Dickert & Bell, 2002; Keßler *et al.*, 2012). Thus, the re-seeding practices occurring in our study area may also affect invertebrate assemblages. If this is the case, lizard persistence in ski resorts may be dependent on the rehabilitation of ski slopes with native plant species including native grasses (e.g. *Poa costiniana*) and shrubs (e.g. *Hovea montana*, *Olearia phlogopappa*), to encourage the re-establishment of diverse invertebrate assemblages (thus food resources) in areas currently dominated by exotic plant taxa. Further, we

suggest retaining native vegetation in future ski run developments, as an alternative to replacement with exotic grasses, will further facilitate this process.

Another reason why rehabilitation of ski slopes using native species may benefit reptiles is that native subalpine vegetation provides more structural complexity than exotic plant species used to stabilise ski runs (e.g. ski runs have a lower abundance and cover of woody plant species that contribute to habitat structural complexity; Wipf *et al.*, 2005). Structural complexity increases the number of niches available in an environment (Macarthur & Macarthur, 1961; Tews *et al.*, 2004), thereby increasing animal diversity and abundance (Tews *et al.*, 2004). Indeed, both *L. guthega* and *P. entrecasteauxii* were strongly associated with habitat features such as rocks and woody debris that are typical of structurally complex habitats. Conversely, removing structural features like vegetation, rocks and woody debris threatens the persistence of these species in the subalpine zone. In particular, rock blasting to create ski runs is likely to have significant impacts on *L. guthega* because it has a restricted geographic distribution of less than 5000 km^2 (TSSC, 2011). Hence, the incremental removal of boulders from ski resorts in a spatially-restricted ecosystem type (i.e. alpine areas comprise 0.15% of terrestrial Australia; Costin *et al.*, 2000) will reduce the extent of suitable habitat for *L. guthega*. Like many other threatened alpine species inhabiting ski resorts (e.g. Patthey *et al.*, 2008; Thiel *et al.*, 2011), this high-altitude specialist is facing a heightened extinction risk if conservation actions like boulder retention, are not implemented.

While the maintenance of structural complexity is important for conserving some subalpine reptiles, our results also show that other species rely on structurally simple habitats. Both *C. praealtus* and *P. pagenstecheri* are specialist species that we observed more frequently in undisturbed grasslands than any other habitat type. They also were negatively associated with structural habitat features (logs, total vegetation cover and understorey shrub cover; Table 2). Clearly, maintaining structural complexity will not benefit the persistence of all subalpine lizards so should not be recommended as a generic management action for conserving reptile

diversity at high-altitudes. Instead, heterogeneity in habitat types is required to accommodate both generalist and specialist lizards (as observed in other landscapes; Pianka, 1996; Benton, Vickery & Wilson, 2003).

We argue that specialist species need to be a focus of further research, as they rely on a narrow range of resources for survival (Preston, 1962). Consequently, the removal of key habitat features in complex or simple environments will threaten these species. However, limited information is available on the fine-scale habitat needs of endemic subalpine lizards, so implementing conservation actions for these assemblages is challenging. For *C. praealtus* and *P. pagenstecheri*, the extent of native grass cover and exotic grass cover (respectively) is an important determinant of distribution, thus the removal and subsequent re-seeding of native grasslands with exotic grass species should be avoided. This is essential for *C. praealtus* because this threatened species has a highly restricted distribution (TSSC, 2009) and relies on a spatially limited habitat type, that is likely to decline in the future due to climate change-related effects (e.g. higher temperatures encouraging the growth of different vegetation forms; see Sebastia, Kirwan & Connolly, 2008).

Conclusions

Subalpine ecosystems are rare environments facing multiple interacting threats of climate change, habitat loss and habitat modification. Animals inhabiting these areas respond idiosyncratically to disturbance, yet limited research is available investigating their responses to disturbance. We have highlighted the importance of retaining structural and compositional habitat features in facilitating the persistence of reptiles in disturbed subalpine areas. However, we acknowledge that further research investigating the efficacy of these actions is urgently needed in subalpine environments.

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Supporting Information

Table S1. Specialist and generalist classifications of the four study species. We categorise reptiles as: 1) common or rare and; 2) specialists or generalists, using six characteristics[a].

	Species			
	C. praealtus	*L. guthega*	*P. entrecasteauxii*	*P. pagenstecheri*
Diet	Unknown – eats invertebrates in captivity	Unknown – assumed to eat invertebrates	Arthropods and other invertebrates	Arthropods and other invertebrates
Distribution	Australian Alps above 1500 m	Australia Alps above 1600 m	Northern NSW to Tasmania and South Australia	Australian Alps as well as plains in Victoria, Tasmania and eastern South Australia
Habitat preferences	Alpine and subalpine grasslands, herbfields, shrublands and woodlands	Alpine and subalpine grasslands, heathlands and woodlands	Forests, woodlands, heathlands, grasslands and alpine herbfields	Grasslands
Specific resource requirements	None identified	Boulders/Rocky outcrops	None identified	Treeless environments preferred
Abundance	Uncommon	Uncommon	Common throughout the Australian snow country	Common throughout the Australian snow country
Conservation Listing	Endangered	Endangered	None	None
Classification	Rare specialist	Rare specialist	Common generalist	Common specialist

[a] Data for this table were collated from Wilson and Swan (2008), Michael and Lindenmayer (2012) and Green and Osborne (2012).

Table S2. Variables included in final HGLMs for each skink species, based on AIC selected best subsets generalized linear models with six predictor variables. The candidate variables we used in the GLMs included: exotic grass cover (EGC), ground layer vegetation density (GLD), ground layer mean vegetation height (GLVH), ground layer shrub cover (GLSC), leaf litter cover (LLC), native grass cover (NGC), total number of rocks between 2-5 m^3 on site (R2-5), total number of rocks greater than 5 m^3 on site (R>5), total number of rocks less than 2 m^3 on site (R<2), number of tree trunks present on site (T), canopy cover (CC), total number of logs on site (TL), total vegetation cover from the ground layer (TVC), total volume of woody debris on site (TVWD), understorey vegetation density (USD), understorey shrub cover (USSC), understorey mean vegetation height (USVH). Selected models are indicated by bold text.

Species	Included Variables	AIC
Cyclodomorphus praealtus	**EGC + LLC + NGC + CC + TL + TVC**	**257.24**
	EGC + LLC + NGC + T + TL + TVC	263.76
	EGC + LLC + T + TL + TVC + USSC	269.22
	EGC + LLC + R2-5 + TL + TVWD + USSC	269.37
	GLD + LLC + T + TL + TVWD + USSC	271.37
	LLC + T + TL + TVC + TVWD + USSC	272.34
	GLSC + LLC + R2-5 + TL + TVWD + USSC	272.79
	GLD + GLVH + TC + TL + USD + USSC	275.90
Liopholis guthega	**EGC + NGC + GLVD + LLC + TVC + R>5**	**312.74**
	EGC + GLVH + GLSC + R2-5 + R>5 + TVC	320.99
	EGC + GLVH + LLC + NGC + TVC + USVH	326.01
	EGC + GLSC + R2-5 + R>5 + T + TVC	327.20
	EGC + GLSC + T + TVC + TVWD + USVH	332.06
	EGC + R2-5 + T + TVWD + USSC + USVH	333.42
	EGC + GLSC + LLC + R2-5 + R>5 + TVC	334.21
	EGC + R>5 + T + TVWD + USSC + USVH	334.91
Pseudemoia entrecasteauxii	**GLMVH + GLSC+ NGC + R>5 + TVWD + USVH**	**255.52**
	GLSC + NGC + R>5 + TL + USD + USVH	258.22
	GLSC + NGC + R>5 + R<2 + TL + USD	258.51
Pseudemoia pagenstecheri	**EGC + GLD + GLSC + R>5 + R<2 + USSC**	**266.73**
	GLVH + GLSC + LLC + R2-5 + R<2 + USSC	265.72
	EGC + GLD + GLSC + R<2 + TVWD + USSC	266.78
	GLVH + GLSC + LLC + R2-5 + R<2 + TVC	267.23
	GLVH + GLSC + LLC + R2-5 + R>5 + TVC	268.57
	GLVH + GLSC + NGC + R>5 + R<2 + USSC	269.09

Table S3. List of dominant plant species retained for the canonical correspondence analysis (CCA).

Scientific Name	Common Name
Agrostis capillaris[a]	Browntop bent
Anthoxanthum odoratum[a]	Sweet vernal grass
Festuca rubra[a]	Red fescue
Empodisma minus	Spreading rope-rush
Epacris glacialis	Reddish bog-heath
Eucalyptus niphophila	Snow gum
Grevillea australis	Alpine grevillea
Hovea montana	Mountain hovea
Nematolepis ovatifolia	Ovate phebalium
Richea continentis	Candle heath
Olearia brevipedunculata	Rusty daisy-bush
Olearia erubescens	Pink-tip daisy-bush
Olearia phlogopappa	Alpine daisy-bush
Oreomyrrhis eripoda	Australian carraway
Orites lancifolius	Alpine orites
Pimelea axiflora	Bootlace bush
Poa costiniana	Bog snow-grass
Prostanthera cuneata	Alpine mint bush

[a] indicates an exotic plant species.

Table S4. Broad-scale habitat associations for four species of skink based on HGLMs (*P. entrecasteauxii* and *P. pagenstecheri*) and GLMs (*C. praealtus* and *L. guthega*). Habitat types are indicated by DG (disturbed grassland), UG (undisturbed grassland), DH (disturbed heathland), UH (undisturbed heathland), DW (disturbed woodland), UW (undisturbed woodland). Blank cells indicate that a habitat type was not included in the model for that species.

	C. praealtus			*L. guthega*			*P. entrecasteauxii*			*P. pagenstecheri*		
	Estimate	SE	*F*, d.f.	Estimate	SE	*F*, d.f.	Estimate	SE	Wald, d.f.	Estimate	SE	Wald, d.f.
DG	-2.71	0.36					-1.43	0.51		-3.41	0.78	
UG	1.98	0.39					1.55	0.68		4.25	0.93	
DH	0.22	0.49	16.68, 5**	-2.15	0.42	11.87, 3***	1.82	0.67	17.86, 5*	0.89	1.01	28.30, 3**
UH	0.81	0.44		1.99	0.45		1.41	0.68		2.50	0.95	
DW	-0.69	0.62		-0.85	0.76		2.48	0.67				
UW	-0.29	0.55		1.69	0.46		2.41	0.66				

*$P<0.05$, **$P<0.01$, ***$P<0.001$.

PAPER III: An Experiment to Test Key Hypotheses of the Drivers of Reptile Distribution in Subalpine Ski Resorts

Prompted by the findings of Paper II, I examine the biotic and abiotic factors that may be underpinning the avoidance of ski runs by reptiles in Paper III. Here, I employ an intervention experiment to determine how a resort management strategy, mowing (i.e. simplification of structural complexity), affects predation risk on plasticine lizard models and thermal regimes

Sato, C.F., Wood, J.T., Schroder, M., Green, K., Osborne, W.S., Michael, D.R. & Lindenmayer, D.B. (2014) An experiment to test key hypotheses of the drivers of reptile distribution in subalpine ski resorts. Journal of Applied Ecology 51: 13-22.

Summary

1. Alpine and subalpine ecosystems support many endemic species. These ecosystems are increasingly under threat from human-induced disturbances such as habitat loss and fragmentation as a consequence of ski resort development and expansion. However, limited peer-reviewed research has investigated the impacts of ski-related disturbances on wildlife, particularly on reptiles.
2. To address this knowledge gap, we conducted reptile surveys to determine the patterns of reptile distribution and abundance in Australian ski resorts. Then, using a factorial experimental design, we investigated: 1) the influence of temperature and predation in driving observed distributions; and 2) how a common ski resort management practice – mowing of modified ski slopes – affected thermal regimes and rates of predation of reptiles on ski runs.
3. We found that the removal of vegetation structural complexity through mowing resulted in significantly higher rates of predation on plasticine models, as well as significantly altered thermal regimes.
4. Crucially, mown ski runs had higher maximum ground temperatures that frequently exceeded the recorded critical maximum body temperatures of the target species of lizards. Thus, mowing has the potential to render these areas unsuitable for thermoregulatory purposes for a large proportion of the potential activity period of reptiles.
5. Together, modifications of the thermal environment and elevated rates of predation appear to explain the avoidance of ski runs by reptiles. To facilitate the persistence of reptiles in disturbed subalpine environments, management plans must focus on implementing strategies that reduce the impact of human activities that alter temperature regimes and predation rates on lizards.
6. ***Synthesis and Applications.*** We suggest that the retention of structural complexity on ski runs (e.g. through the cessation of mowing during peak reptile activity periods) and/or revegetation with native plant communities will concurrently provide refuge from predators

and buffer against extreme temperatures, making ski runs more hospitable to reptiles. Based on our findings, we emphasize that effective management strategies targeting subalpine biodiversity conservation require an understanding of the drivers that determine species distributions in these landscapes.

Keywords: *grasslands, high altitudes, lizards, mowing, predation risk, ski run, skinks, temperature regimes*

Introduction

Alpine and subalpine ecosystems are significant for biodiversity and support high levels of endemic taxa due to the unique climatic characteristics and geographical isolation (Körner 2004; Nagy & Grabherr 2009). However, the biodiversity found in alpine and subalpine ecosystems is affected globally by major ski developments. There are around 6000 ski resorts and ski areas across the globe, with extensive developments in Europe, Canada, USA and Japan (Vanat 2012). Cumulatively, these ski developments can significantly degrade and fragment alpine and subalpine habitats, threatening the persistence of wildlife in affected environments [WWF (World Wide Fund for Nature) 2005].

The development of ski resorts has a major impact on high mountain environments (WWF 2005) and arguably the greatest impact is from the construction of groomed ski slopes and ski runs (Wipf *et al.* 2005; Negro *et al.* 2010; Caprio *et al.* 2011). For example, in many North American and Australasian ski areas, native vegetation, rocks, logs and woody debris are removed and soils are extensively compacted during initial construction of groomed ski runs (Ries 1996). The runs may then be seeded with exotic grass species to aid slope stabilization (Tsuyuzaki 1994). During winter, slope grooming is conducted, and mowing is carried out during spring and summer maintenance (one to four times per year; Strong, Dickert & Bell 2002; Kubota & Shimano 2010) to inhibit the establishment of woody vegetation, facilitate

early snow coverage, and reduce the demand for snowmaking during the winter ski season [PBPL (Perisher Blue Pty Ltd) 2002; Strong, Dickert & Bell 2002]. These activities greatly reduce the structural complexity of the vegetation and ground cover of ski runs and, in turn, affect the distributions and survival of wildlife inhabiting these areas (Laiolo & Rolando 2005; Negro *et al.* 2009).

Indeed, in a previous study, we found that lizard abundance was greatly reduced on ski runs and this was due – in part – to the removal of rocks, woody debris and tussock grasses (i.e. structural complexity; Chloe F. Sato, unpublished data). However, studies investigating the impacts of ski runs on reptiles are limited (Sato, Wood & Lindenmayer 2013). Thus, the effects of ski run construction and maintenance on underlying ecological drivers important to reptile survival remain unknown.

In other ecosystems, disturbances resulting in the simplification of habitat structural complexity modify underlying biotic processes (e.g. rates of predation and availability of prey; Babbitt & Tanner 1998) as well as abiotic factors (e.g. microclimates; Webb, Shine & Pringle 2005) that directly influence reptile survival (Pianka & Pianka 1970; Huey & Slatkin 1976). However, for subalpine reptiles, the direct and indirect effects of altering habitat complexity may be more pronounced than for faunal communities occurring at lower altitudes. This is because, at higher elevations, reptiles must balance the risk of predation with the need to thermoregulate (usually through direct basking) in extreme and highly variable environmental conditions (Sandercock, Martin & Hannon 2005; Huang & Tu 2008). If reptiles in these ecosystems do not take the opportunities to bask when thermal conditions are optimal, they will not maximise energy assimilation and will fail to maximise growth, time spent foraging, or time spent seeking mates (Martin & Salvador 1993; Martin & Lopez 1999; Webb & Whiting 2005). However, basking poses a significant risk to immediate survival as, for many subalpine reptiles, basking opportunities coincide with peak activity periods of predators such as corvids and raptors (Baker-Gabb 1984; O'Brien *et al.* 2010). Consequently, structural complexity may be crucial to

the long-term persistence of reptiles by moderating rates of predation (Stamps 1983; Rubbo *et al.* 2001; Amo, Lopez & Martin 2007).

Despite the importance of habitat structural complexity in moderating abiotic and biotic processes influencing subalpine reptiles, experimental studies investigating the inter-relationships between these factors are strikingly limited. In this paper, we address this knowledge gap by quantifying the mechanisms underpinning ski run avoidance by lizards. We suggest that two possible drivers related to structural complexity – predation and thermal environments – may strongly influence observed patterns of lizard distribution (see Fig. 1).

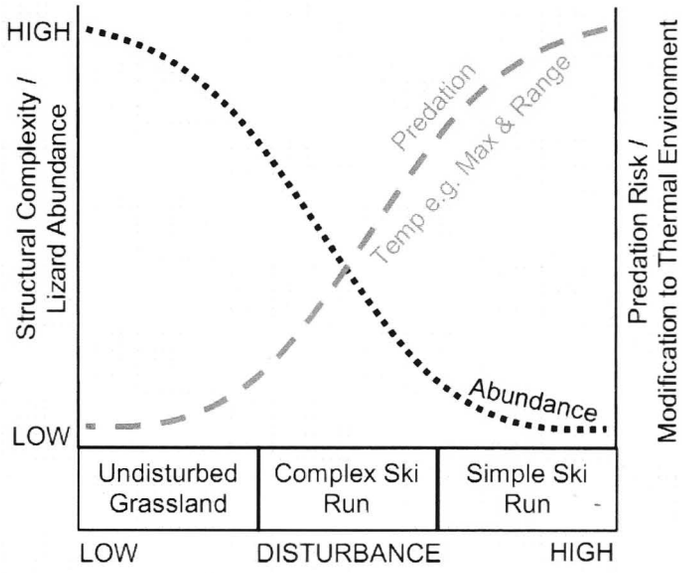

Figure 1. Conceptual summary of the hypothesized relationships between lizard abundance, structural complexity, predation and temperature in subalpine habitats with differing levels of disturbance.

Hypothesis 1 - Predation

We postulated that the reduction of habitat structural complexity on ski runs could potentially increase rates of predation on reptiles because individuals basking on, or dispersing across, these areas are more visible to predators. Several studies suggested that rates of predation increase for a suite of different taxa as habitat structure is removed (see Irlandi 1994; Babbitt & Tanner 1998; Arthur, Pech & Dickman 2005) and animal behaviour is altered to compensate for this increased predation risk (or perception thereof; Cuadrado, Martin & Lopez 2001; Lopez &

Martin 2013). Hence structural complexity plays an important role in providing protection from predators and reducing perceived predation risk, and this could be driving the distributions of reptiles in subalpine ski resorts and adjacent areas.

Hypothesis 2 – Thermal Environments

We postulated that the thermal regime of ski runs dominated by exotic grasses would be altered as structural complexity was reduced. In some instances, the alteration of thermal environments can benefit reptiles as thermoregulatory opportunities may be increased (Huey & Slatkin 1976; Langkilde, O'Connor & Shine 2003). However, we argue that the extreme simplification of habitat structure may fundamentally degrade the thermal quality of grassland habitats for lizards, as intensively disturbed ski runs lose their ability to buffer against extreme temperatures. As a consequence, substrate temperatures may rise to levels much higher than the critical maximum body temperatures of lizards inhabiting subalpine environments (see Spellerberg 1972). This would limit lizard activity periods to earlier or later in the day, potentially preventing sufficient periods for energy assimilation (Huey & Slatkin 1976; Huey, Losos & Moritz 2010) and exposing animals to greater risk of predation (Fox 1978). Due to thermal constraints on intensively modified ski runs, lizards may avoid these habitats in preference for other, more thermally suitable environments.

By testing these two important hypotheses, this paper contributes to our understanding of the key constraints that drive reptile distributions in disturbed subalpine ecosystems. Our findings reveal that both temperature regimes and rates of predation can be significantly affected by human activities and that together these drivers provide a compelling explanation for the avoidance of modified ski runs by reptiles. Based on these important new insights, we propose measures to mitigate potential negative effects of habitat modification on reptile assemblages occurring in and around ski resorts.

Materials and Methods

Study Species

Our intervention experiment investigated the effect of habitat structural complexity on two key ecological drivers, thermal environments and predation, which may regulate the occurrence of reptiles in disturbed grasslands on ski runs and in undisturbed grasslands. Accordingly, we selected two grassland-associated reptile species for our experiment. Both alpine she-oak skink *Cyclodomorphus praealtus* and grassland tussock skink *Pseudemoia pagenstecheri* are diurnally active heliotherms (Spellerberg 1972) that have strong associations with grassland or grassy-heath matrix environments (Green & Osborne 2012), and have been detected previously in skiing areas (C.Sato; unpublished data). Both species occur in the Australian subalpine region. However, *C. praealtus* is found only at elevations above 1500 m in the Australian Alps (Green & Osborne 2012) while *P. pagenstecheri* occurs more widely across south-eastern Australia (Wilson & Swan 2008). The thermal physiology of these lizards has not been specifically investigated but one closely related sympatric species (woodland tussock skink *Pseudemoia entrecasteauxii*) can tolerate a wide range of body temperatures (T_{min} = 2.2–2.8°C, T_{max} = 41.9–42.5°C; Spellerberg 1972), as can a larger bodied sympatric species – alpine water skink *Eulamprus kosciuskoi* (T_{min} = 2.0-3.2°C, T_{max} = 39.8-40.8°C; Spellerberg 1972). Given the range of temperatures that *P. entrecasteauxii* and *E. kosciuskoi* can endure, it is likely that the critical body temperatures of *C. praealtus* and *P. pagenstecheri* fall somewhere within this range.

The diet of *C. praealtus* and *P. pagenstecheri* is assumed to consist predominantly of invertebrates (Green & Osborne 2012) but vegetation also may be consumed opportunistically (Brown 1991). Invertebrates are abundant in alpine and subalpine areas, including in disturbed grasslands that have been developed for skiing (Hammelbacher & Mühlenberg 1986; Negro *et al.* 2009; Rolando *et al.* 2012), and therefore are not likely to be limiting to reptiles living at high altitudes.

Study Area

We conducted our study in and around the largest alpine–subalpine resort complex in Australia, Perisher ski resort (36°24'S 148°24'E; PBPL 2002). The resort is located in Kosciuszko National Park, south-eastern Australia (Fig. 2a). Our grassland survey areas in the national park were characterised by native grasses [predominantly *Poa costiniana* (Vickery) and *Rytidosperma nudiflorum* (P. Morris)] and herbs [such as *Empodisma minus* (Hook.f.); Costin *et al.* 2000]. Within Perisher Ski Resort, our survey areas were located on subalpine ski slopes dominated by exotic grasses [predominantly *Agrostis capillaris* (Boiss. & Reuter) and *Festuca rubra* (L.)]. The ski slopes were almost entirely covered by exotic grasses with occasional patches of bare ground. Mean mid-summer shade temperatures are about 10°C (but can reach maxima around 30°C; BOM 2013), while daily mean winter temperatures are around -5°C (Costin *et al.* 2000; Green & Osborne 2012). Annual precipitation is greater than 2000 mm per year with summers usually drier than winters (Green & Osborne 2012) and snow covering the area from mid-June to October.

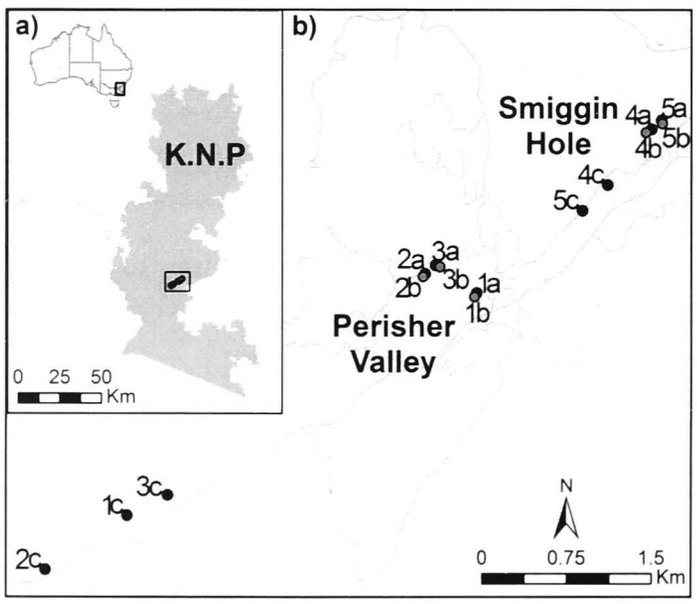

Figure 2. (a) Map of the study area in Kosciuszko National Park, south-eastern Australia. (b) Location of the replicate 'blocks' within Kosciuszko National Park. Each marker indicates an individual site; numbers above markers indicate a 'block' of sites (e.g. 1=Perisher 1; 2=Perisher 2; 3=Perisher 3; 4=Smiggin 1; 5=Smiggin 2); letters above markers indicate grassland types within blocks (e.g. a=unmown; b=mown; c=undisturbed). Grey lines designate roads.

Experimental Design

We established a blocked experiment comprised of subalpine grassland habitats only, in two disturbance categories (disturbed/undisturbed). We located the disturbed grassland sites in the centre of ski runs within the lease areas of Perisher Ski Resort. These sites had been cleared of vegetation, graded by heavy machinery, and then rehabilitated with a mix of exotic grasses (predominantly *A. capillaris* and *F. rubra*). We located undisturbed examples of grasslands outside Perisher Ski Resort. These sites exhibited minimal or no signs of disturbance from ski resort development.

We selected sites to enable a full experimental factorial design, yielding three 'treatments': 1) undisturbed grasslands, 2) 'complex ski runs' where some structural complexity was retained by leaving long exotic grasses (~28cm) intact on the ski run, and 3) 'simple ski runs' that displayed minimal structural complexity after grass was slashed using a 'Whipper Snipper' to ~4cm above ground level. We replicated the three treatments five times in complete replicate blocks, giving a total of 15 sites (Fig. 2b). We ensured that all sites were 5 x 40 m rectangular plots located on south-facing slopes between 1700–1830 m a.s.l.

Lizard Models

Plasticine models have been used previously in many different ecosystems to estimate rates of predation (see Niskanen & Mappes 2005; Vervust, Grbac & Van Damme 2007; Daly, Dickman & Crowther 2008). We constructed models of adult *C. praealtus* and *P. pagenstecheri* using non-toxic sculpting clay (Monster Clay; The Monster Makers, Ohio, USA) using mean morphological measurements from specimens caught in the field (*C. praealtus*: n = 30, *P. pagenstecheri*: n = 43; Chloe F. Sato, unpublished data). After construction, we painted the models using non-toxic paint to approximate the true colouration of each species (Fig. 3). In total, we created 100 replica models of each species for use in our study.

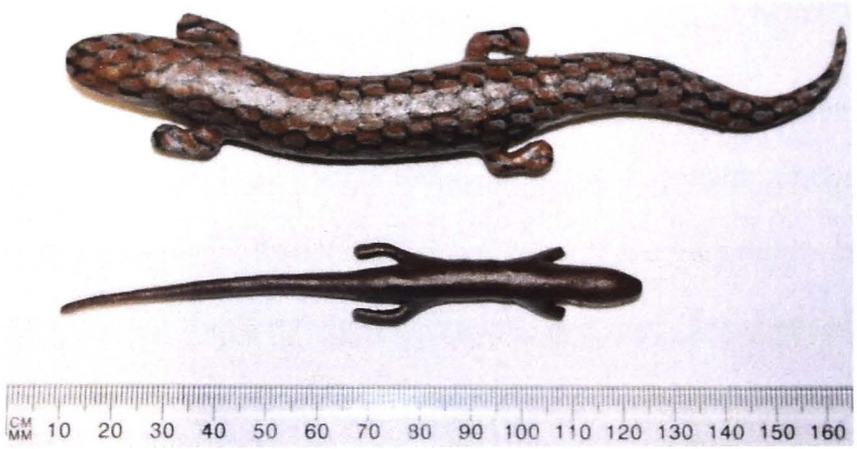

Figure 3. Lizard models used in predation experiment (to scale). The larger-bodied lizard represents *C. praealtus* and smaller-bodied lizard represents *P. pagenstecheri.*

Estimating Rates of Predation on Lizards

To test Hypothesis 1 (Predation), we established baseline predation rates in each treatment (i.e. undisturbed grassland; complex ski run; simple ski run) before mowing, between 10 January and 14 January, 2013. To do this, we placed five plasticine models of each species (*C. praealtus* and *P. pagenstecheri*) along a 40-m transect at each site (i.e. 10 models in total at a site, 150 models in total across all sites). We positioned models among (but not completely obscured by) grasses at 4-m intervals along each transect, alternating examples of *C. praealtus* and *P. pagenstecheri*. We placed a single camera trap (Scout Guard KG680V; Faunatech Pty Ltd, VIC, Australia; height, 140 mm; width, 102 mm; depth, 74 mm) on each transect to identify the types of predators that were present near the models over approximately four days (99 hours), before scoring predation attempts. We considered a predation attempt to include the displacement of the model from the transect, complete removal of the model from the site, or visible signs of attack (e.g. bite, scratch or claw marks) on the model. For each model, we recorded: 1) whether the model had been attacked, 2) the evidence for predation (e.g. displacement, removal or visible signs of predation), 3) where on the model scratch, bite or claw marks were located, and 4) the type of predator that had attacked the model.

After scoring all the predation attempts along a transect, we reset camera traps and replaced lizard models at undisturbed grassland and complex ski run sites. At simple ski run sites, we

removed all models from the transect then mowed the grass to ground level (i.e. <5cm height) 2.5 m either side of the transect. After mowing, we reset camera traps and replaced the models along the transect, as before. We left all models and camera traps for a further four days (99 hours) between January 14 and January 18 2013, before scoring the new models for predation attempts.

Thermal Environments in Grasslands

To test Hypothesis 2 (Thermal Environments), we used temperature loggers (Thermochron i-Buttons, Thermodata Pty Ltd, QLD, Australia; diameter, 17.4 mm; height, 5.9 mm) to record the range of ground surface temperatures available to lizards in grassland sites while running our plasticine model experiment. We deployed three temperature loggers at each site where we set plasticine models. We placed one temperature logger at either end of the 40-m transect and one at 20 m, ensuring that the loggers were in contact with the ground but partially covered by grasses to prevent exposure to lengthy periods of direct sunlight. We offset all loggers two metres from the transect to avoid disturbance by animals preying on plasticine models. We programmed loggers to record temperature every 30 minutes and left the loggers in situ for the duration of the experiment (i.e. January 10th to January 18th). After eight days, we collected all loggers for analysis.

Statistical Analysis

To explore the effect of structural complexity on predation rates, we fitted Hierarchical Generalised Linear Models (HGLM; Lee, Nelder & Pawitan 2006) to the numbers of models attacked for each 'species' separately and for all models regardless of species. We assumed a quasi-binomial distribution with a logit link function for the response and a beta-distribution with a logit link function for the random component. We included 'Mowing Intervention' (i.e. before mowing or after mowing) and 'Site' (i.e. undisturbed grassland, complex ski run or simple ski run) as fixed effects and 'Treatment' nested within 'Block' as random effects to account for the spatial structure in the data.

To analyse temperature data, we included temperature readings taken between 05:00 and 18:30 (Australian Eastern Standard Time, 'AEST') when lizards were likely to be active. For these readings, we calculated the mean, absolute maximum, absolute minimum, and range of ground surface temperatures recorded at each data logger, in each grassland type, over the four-day periods before and after mowing. We then used an analysis of variance (ANOVA) to determine whether there were any significant changes in the thermal environments of different grassland types before and after our experimental intervention (mowing).

Finally, we determined the total number of hours that ground surface temperatures exceeded the absolute critical maximum and minimum body temperatures of sympatric lizards (an absolute critical minimum of 2°C for *E. kosciuskoi* and an absolute critical maximum of 42.5°C for *P. entrecasteauxii*; Spellerberg 1972), as a proportion of the total number of hours available for lizard activity (14 hours), before and after our mowing intervention. We then fitted a quasi-binomial HGLM to investigate whether the calculated proportion of hours differed between treatments, before and after mowing. We included Site and Mowing Intervention as fixed effects, with the proportion of hours as the response variable. To account for the spatial structure, we included Day as well as Logger Position and Treatment nested within Block as random effects.

We used Genstat 15 (VSN International Ltd) for all statistical computation.

Results

Rates of Predation

During the plasticine predation experiment, the camera traps recorded red deer *Cervus elaphus*, European hares *Lepus europaeus*, Australasian pipits *Anthus novaeseelandiae* masked lapwings *Vanellus miles*, little ravens *Corvus mellori*, Australian ravens *Corvus coronoides* and European red foxes *Vulpes vulpes*. Three of these species are known predators of subalpine lizards in

Kosciuszko National Park: *C. mellori*, *C. coronoides* and *V. vulpes* (Green & Osborne 1981; Green 2003). However, based on camera trap footage and markings on plasticine models, we conclude that corvids (*C. mellori* and *C. coronoides*) were the only predators of our lizard models. Markings consisted of beak and claw marks, predominantly located on the head (n = 36), trunk (n = 32) and tail (n = 24) of models (see Fig.4 for examples). We did not observe mammalian or reptilian predatory attempts.

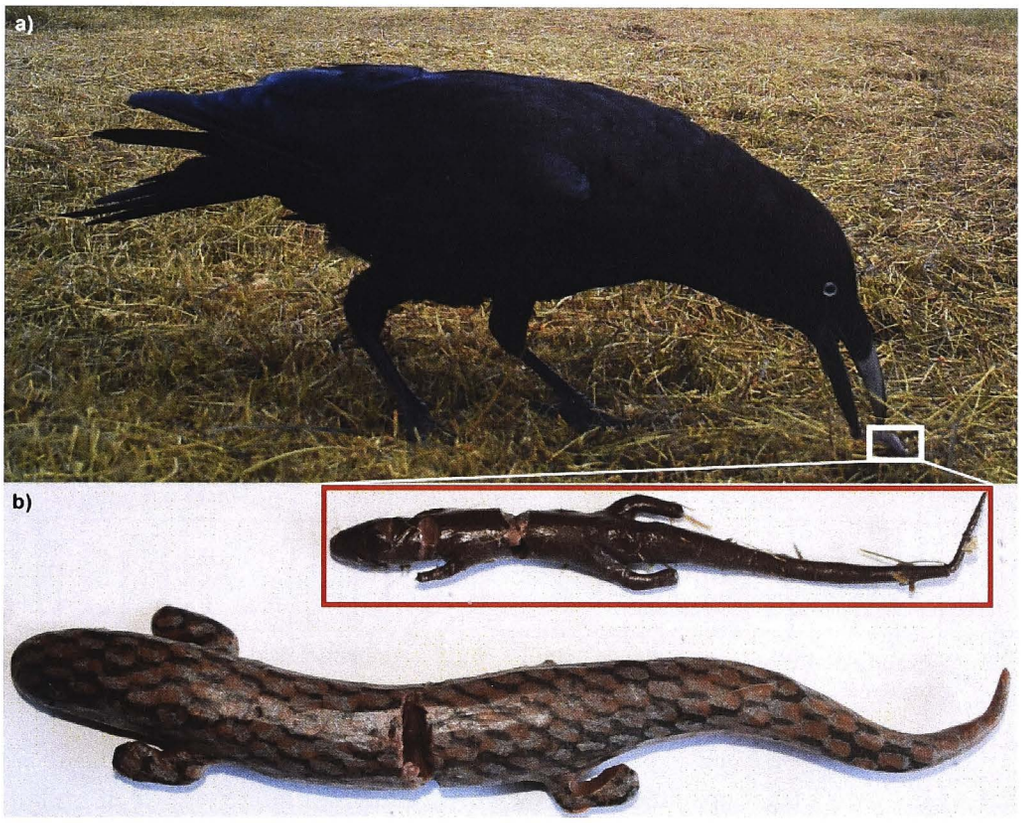

Figure 4. Examples of predation on lizard models. (a) Camera trap image showing *C. coronoides* preying on a 'lizard' in the field; (b) Examples of the types of markings observed on models from corvid predation attempts. Upper lizard depicts the model highlighted in (a).

Before mowing, rates of predation on the models were not significantly different between grassland treatments for either species, or when species were pooled (Fig. 5). After mowing, the rates of predation were altered in each treatment, with the lowest levels of predation occurring in undisturbed grasslands and the highest levels occurring on structurally simple (mown) ski runs (Fig. 5). For individual species, the interaction between mowing intervention and treatment was not significant (*C. praealtus*: $\chi^2_2 = 3.935$, $P = 0.14$; *P. pagenstecheri*: $\chi^2_2 = 3.505$, $P =$

0.173). However, when predation data were pooled for both species, the interaction was significant ($\chi^2_2 = 7.989$, $P = 0.018$; a complete table of estimates from the HGLMs is provided in Table S1 in Supporting Information). This indicates that sites which were mown had significantly higher overall rates of predation compared with baseline (pre-mowing) levels (Fig. 5c). Where structural complexity was not reduced [i.e. undisturbed grassland and unmown (complex) ski runs], overall rates of predation did not differ significantly with intervention (Fig. 5c). Interestingly, predation rates in the undisturbed grasslands were lower after the mowing intervention (Fig. 4) suggesting that corvids learnt that models were inedible in these locations or that the birds may have been attracted to calls from conspecifics at nearby resorts (Bugnyar, Kijne & Kotrschal 2001) where prey items were more obvious due to mowing.

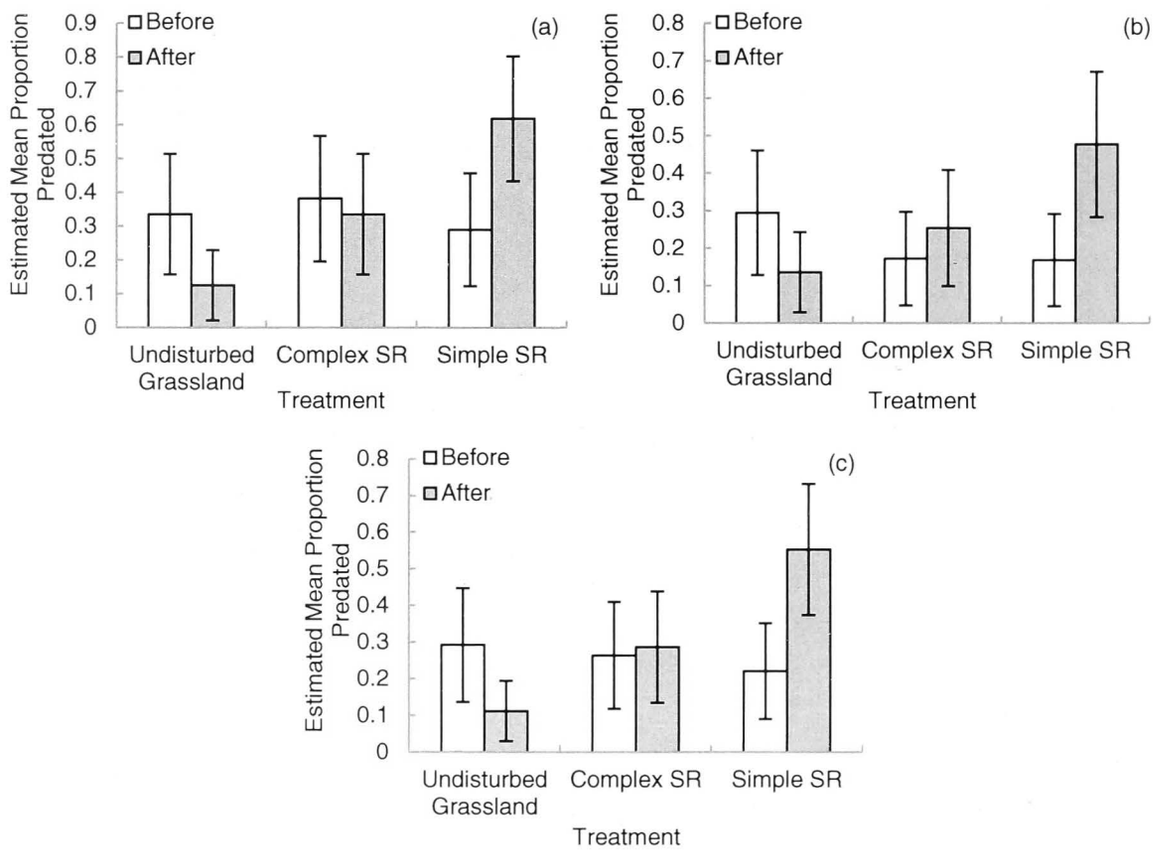

Figure 5. Estimated mean proportions (±SE) of predation attempts on plasticine models in undisturbed grasslands and on ski runs ("SR"), for all models and by individual species. (a) Predation of *C. praealtus* models, (b) Predation of *P. pagenstecheri* models, and c) All predation attempts pooled.

Thermal Environments

Before the mowing intervention, both simple and complex ski runs had higher mean, maximum and minimum ground temperatures than undisturbed grasslands (Table 1). In addition, ski runs had a greater range of ground temperatures compared to undisturbed grasslands (Table 1). We observed these same ground temperature patterns after mowing (Table 1). However, in areas where extreme simplification of structural complexity was undertaken (i.e. simple ski runs), mean and maximum ground temperatures were significantly higher, and the range of ground temperatures was significantly greater, than in undisturbed grasslands (Table 1). Mean and maximum ground temperatures on simple ski runs also were higher than on complex ski runs (Table 1), but this difference was not significant.

Table 1. Mean, maximum, minimum and range of temperatures recorded (with least significant differences; 'l.s.d') in undisturbed grasslands (C), complex ski runs (CSR) and simple ski runs (SSR), before and after mowing had occurred

	Before Mowing			**After Mowing**			**l.s.d**		
Temperature Measure (°C)	C	CSR	SSR	C	CSR	SSR	Same level of treatment	All other comparisons	F
Mean	16.6	20.0	20.0	19.1	22.4	26.2	1.13	2.94	$F_{2,42} = 14.64$***
Maximum	35.4	38.8	39.9	35.0	38.6	47.1	3.08	6.01	$F_{2,42} = 8.08$**
Minimum	-2.7	0.9	0.8	-1.1	1.6	-0.2	1.10	2.88	$F_{2,42} = 5.91$**
Range	38.1	37.9	39.1	36.1	37.0	47.3	3.63	7.03	$F_{2,42} = 9.72$***

*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$

We also found that mowing altered the length of time that ground temperatures exceeded the critical maximum body temperatures of lizards. Before mowing, there were no significant differences between grassland types in the length of time exceeding the critical maximum body temperatures of lizards (control: 0.29 ± 0.21 h day^{-1}; complex: 0.44 ± 0.17 h day^{-1}; simple: 0.45 ± 0.23 h day^{-1}). However, after mowing, sites with grass removed had significantly longer periods where ground temperatures exceeded the critical maximum body temperatures of lizards (undisturbed grassland: 0.12 ± 0.12 h day^{-1}; complex ski run: 0.49 ± 0.25 h day^{-1}; simple ski run: 2.20 ± 0.45 h day^{-1}; $\chi^2_2 = 75.45$, $P < 0.001$; Fig. 6). The length of time that ground temperatures

exceeded the critical minimum body temperatures of lizards was not significantly different between grassland types, before or after mowing ($\chi^2_2 = 3.701$, $P = 0.157$; a complete table of estimates from the HGLMs is provided in Table S2).

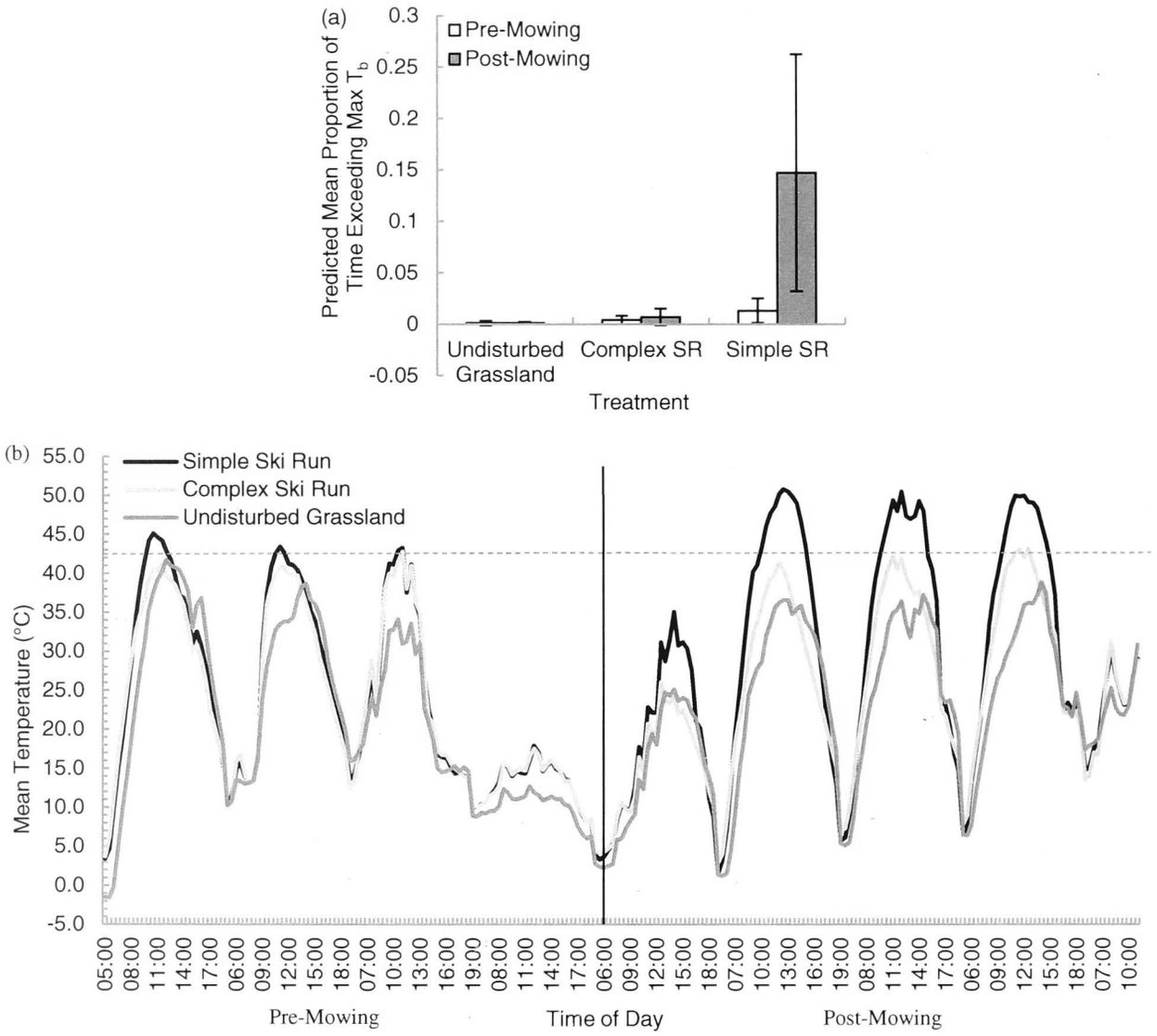

Figure 6. (a) Predicted mean proportion of time (±SE) that surface ground temperatures exceeded the critical maximum body temperature (T_b) of lizards in three grassland types, before and after mowing. (b) Mean absolute maximum ground surface temperatures (°C) recorded in three grassland types during lizard activity periods, before and after mowing. The 'time of day' is reported as Australian Eastern Standard Time (AEST). The dashed horizontal line represents the absolute critical maximum body temperature of a sympatric lizard (*P. entrecasteauxii*) recorded by Spellerberg (1972).

Discussion

In this paper we sought to determine whether two key ecological drivers – thermal environments and predation – are affected by the removal of structural complexity (through

mowing), and consequently contribute to the distributions of reptiles in subalpine grasslands observed in a previous study (Chloe F. Sato; unpublished data). We found that both thermal regimes and rates of predation were significantly affected by the removal of structural complexity. Overall rates of predation were significantly higher on ski runs where structural complexity was removed (Fig. 5). In addition, the absolute maximum and mean ground temperatures were higher on simple ski runs, and exceeded the critical maximum body temperatures of lizards for longer periods, than either complex ski runs or undisturbed grasslands (Table 1 and Fig. 6). As both thermal regimes and predation are key drivers that can affect the survival of reptiles in the short and long-term (Martin & Lopez 1999; Webb & Whiting 2005), we argue that these drivers contribute to the avoidance of mown ski runs by lizards.

The thermal environment is an important determinant of reptile occurrence (Webb & Whiting 2005; Daly, Dickman & Crowther 2008). Our results indicate that the removal of grassland structural complexity had a dramatic effect on ground temperatures. While reptiles are well adapted behaviourally and physiologically to cope with thermal variability (Huey, Losos & Moritz 2010), the extreme maximum ground temperatures that occur on mown (simple) ski runs preclude the use of these habitats by lizards for extended periods of the day. As vegetation is reduced to a short herbaceous layer by mowing (i.e. low structural complexity), lizards cannot modify their behaviour to avoid these extreme temperatures by positioning themselves higher in the vegetation or by seeking refuge under cover objects or in areas of shade (Huey 1974). Consequently, simplified ski runs heighten the risk of overheating while foraging, thermoregulating or finding mates, especially during hotter periods of the day. Even though the unmown (complex) ski run still comprises a single herbaceous layer, the increased height and density of the grass resulted in considerable thermal buffering (Fig. 6).

In addition to sub-optimal thermal environments, the unsuitability of mown (structurally simple) ski runs is further increased by elevated risks of predation. The extreme simplification of these

areas provides no refuge from predatory attempts. Thus, reptiles are likely to perceive the ski runs as high-risk, low-quality habitat. Indeed, the increased perception of predation risk by lizards on ski runs is supported by Amo, Lopez & Martin (2007) who found that lizards moved further and at greater speeds on ski runs in Europe, in response to the low availability of refuges. Additionally, this risk of predation (and the perception of this risk; Lima 1993) is likely to increase as the width of the ski runs increases, because lizards will have to travel further to reach refuges. For large-bodied reptiles (and gravid females) this is particularly important because: 1) they may be more susceptible to predation by avian predators that select for larger-bodied individuals during bird breeding seasons (Padilla, Nogales & Marrero 2007); and 2) ski resorts encourage larger concentrations of scavenging birds (Storch & Leidenberger 2003; Jokimaki *et al.* 2007) that also may prey on lizards in the area. Thus, to facilitate the movements of reptiles throughout disturbed ski resorts, it is essential that additional cover is available on ski runs. Our results indicate that even the absence of mowing provided enough cover to significantly reduce rates of predation. Hence measures to maximise complexity – such as the cessation of mowing and/or the rehabilitation of native forbs and grasses on ski slopes - will enhance disturbed areas for reptiles.

From our field observations (Chloe F. Sato, unpublished data), we suggest that lizards in ski resorts are favouring alternative habitats to mown ski runs (such as rock outcrops, woodlands, heathlands or undisturbed natural grasslands) where structural complexity is higher and opportunities exist for shuttling between areas of shade and sun. These habitats provide additional cover for avoiding predators, and a greater opportunity to avoid extended exposure to extreme temperatures. The selection of habitats other than structurally simple (mown) ski runs by lizards does not pose a threat to their persistence in these disturbed subalpine landscapes. However, if ski resorts continue to expand and new ski runs are constructed using current slope grooming practices, habitat will increasingly be fragmented and the remaining patches utilised by lizards will progressively become more isolated from one another. As lizards generally have low dispersal abilities (e.g. between 20 m and 57 m depending on the species; see Clobert *et al.*

1994; Olsson & Shine 2003), mown ski runs with widths greater than 20 m have the potential to seriously inhibit lizard movement and dispersal, particularly during the summer and autumn months when reproduction and dispersal of young is occurring (Green & Osborne 2012). However, there have been very few studies of lizard movement patterns in alpine or subalpine environments (but see Amo, Lopez & Martin 2007), so it is possible that 20 m is an under- or over-estimate of what constitutes a barrier to dispersal, especially considering the effect that factors such as body size, age and sex have on dispersal ability (Olsson & Shine 2003; Warner & Shine 2008).

Clearly, it is important that we begin to consider how the management of ski runs affects underlying ecological processes and constraints as, at present, it is likely that modified ski runs are having significant negative effects on reptiles in affected areas. These impacts may increase with the alterations in thermal regimes associated with climate change. Higher ambient temperatures will lead to higher ground surfaces and a reduced time for reptiles to forage and thermoregulate within their operative temperatures (Huey, Losos & Moritz 2010). This will result in reptiles assimilating less energy for the purposes of foraging, reproducing and avoiding predation (Huey & Slatkin 1976). Higher ambient temperatures also could result in increased predator densities at higher altitudes (Green 2006). As the duration of snow cover decreases, territorial birds that prey on reptiles but are currently restricted to lower elevations (e.g. laughing kookaburra *Dacelo novaeguineae*) may begin to establish territories at higher elevations (Green 2006). Hence, it is imperative that we further map reptile distribution patterns in subalpine and alpine environments and better elucidate the underlying processes giving rise to these patterns, so we are equipped to effectively manage reptile diversity in these areas, now and in the future.

Management Implications

Temperature regimes and rates of predation together provide a compelling explanation for the avoidance of modified ski runs by reptiles. While our results are only directly applicable to

Perisher Ski Resort, they also are of importance to ski resorts with similar management practices and similar assemblages of predators. As such, we recommend that to facilitate the persistence of reptiles in disturbed subalpine environments, management plans must focus on implementing strategies that reduce the impact of these key environmental drivers. Our results show that rates of predation were lowest and the thermal environment was most conducive to lizard activity in undisturbed grasslands. It is also in these environments that lizard abundances were highest (Chloe F. Sato; unpublished data). Based on this information, we suggest that undisturbed grasslands located in ski resort lease areas should be preserved wherever possible to facilitate the persistence of reptiles, particularly grassland specialists. There also may be a need to revegetate ski slopes with native plant species to restore linkages between otherwise presently fragmented habitat. This may be imperative for threatened species that have limited distributions such as *C. praealtus* (TSSC 2009).

Where undisturbed grasslands cannot be retained or are already highly modified, we suggest that the retention of structural complexity on ski runs (e.g. through the cessation of mowing at the very least during peak reptile activity periods) will concurrently provide refuge from predators and buffer against extreme temperatures, making ski runs more hospitable to reptiles. We advise against the intensive management of ski runs (e.g. mowing, slope grooming and vegetation removal), particularly when reptiles are reproductively active and when young are likely to be dispersing during the warmer spring and summer months. We also advise that the development of future ski runs includes the retention of low growing native plant species and the avoidance of exotic grasses in revegetation.

Conclusions

The effective management of reptile biodiversity in disturbed subalpine landscapes requires an understanding of the ecological constraints driving observed patterns of distribution and abundance. Our study has demonstrated that two key ecological drivers – predation and thermal

environments – can be significantly affected by human intervention. In turn, this degrades the quality of grassland habitats on ski runs for reptiles. Based on our results, we suggest that the retention of structural complexity on ski runs will concurrently provide refuge from predators and buffer against extreme temperatures, making ski runs more hospitable to reptiles.

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Supporting Information

Table S1. Table of estimates from HGLMs for rates of predation on *Cyclodomorphus praealtus* models and *Pseudemoia pagenstecheri* models separately, and together (i.e. all predation attempts pooled), in three different grassland treatments.

	C. praealtus			*P. pagenstecheri*			All models		
	estimate	s.e.	d.f., Wald	estimate	s.e.	d.f., Wald	estimate	s.e.	d.f., Wald
Constant	-0.69	0.80		-0.88	0.80		-0.89	0.75	
Post-mowing	-1.26	1.01		-0.98	0.96		-1.19	0.70	
CSR[a]	0.20	0.87	2, 3.935	-0.69	0.97	2, 3.505	-0.14	0.78	2, 7.989*
SSR[b]	-0.21	0.89		-0.72	0.97		-0.38	0.79	
Post-mowing.CSR	1.05	1.34		1.47	1.35		1.30	0.94	
Post-mowing.SSR	2.63	1.35		2.49	1.33		2.66	0.94	

[a] CSR = Complex (unmown) ski run, [b] SSR = Simple (mown) ski run; *$P<0.05$

Table S2. Table of estimates from HGLMs for the proportion of time that ground surface temperatures exceeded the critical minimum and critical maximum body temperatures of a sympatric subalpine lizard, in three different grassland treatments.

	Time Exceeding Max. T_b			Time Exceeding Min. T_b		
	estimate	s.e.	d.f., Wald	estimate	s.e.	d.f., Wald
Constant	-6.51	1.10	2, 75.45*	-8.68	1.90	2, 3.701
CSR[a]	-0.86	1.08		-1.79	0.65	
SSR[b]	2.21	0.98		-1.36	0.62	
Post-Mowing	-0.40	1.04		5.17	2.30	
Post-mowing.CSR	1.16	0.42		-0.03	0.25	
Post-mowing.SSR	2.94	0.40		0.40	0.22	

[a] CSR = Complex (unmown) ski run, [b] SSR = Simple (mown) ski run; *P<0.001

PAPER IV: Designing for conservation outcomes: The value of remnant habitat for reptiles on ski runs in subalpine landscapes

Reptiles largely avoid ski runs in alpine-subalpine environments, due to considerable alterations to vegetation composition, structural complexity, thermal regimes and rates of predation. However, patches of remnant vegetation are often retained on ski runs and may be capable of supporting populations of lizards or, alternatively, could act as stepping stones between disconnected areas of continuous forest. In this paper, I investigate the value of vegetated patches on ski runs for reptiles within the framework of habitat fragmentation theory.

Sato, C.F., Wood, J.T., Schroder, M., Michael, D.R., Green, K. & Lindenmayer, D.B. (in press) Designing for conservation outcomes: The value of remnant habitat for reptiles on ski runs in subalpine landscapes. Landscape Ecology.

Abstract

Subalpine ecosystems are centres of endemism that are important for biodiversity. However, these areas are under threat from the creation, expansion and continued modification of ski runs, activities that have largely negative effects on wildlife. Despite this threat, research on the impacts of ski runs is limited for reptiles - particularly regarding the value of remnant vegetation retained on ski runs. Here we quantify the effects of habitat loss and fragmentation (i.e., patch size, patch isolation and edge effects) on the abundance of a common subalpine lizard and on thermal regimes (a key determinant of lizard distribution) in an Australian ski resort. The number of lizards observed differed significantly with habitat type (ski runs vs. forested areas) and patch isolation, but not patch size. In addition, the edges of patches supported more lizards than any other habitat type. These patterns of lizard distribution can be explained, in part, by the differing thermal regimes in each habitat. Ski runs had significantly higher ground surface temperatures than any other habitat type, precluding their use for a considerable proportion of the activity period of a lizard. In comparison, edges were characterised by lower temperatures than ski runs, but higher temperatures than the core of forested areas, potentially providing a favourable environment for thermoregulation. Based on our results, we conclude that although modified ski runs have a negative effect on lizards, patches of remnant vegetation retained on ski runs are of value for reptiles and their conservation could help mitigate the negative effects of habitat loss caused by ski run creation.

Keywords: *edge effects; habitat loss; habitat fragmentation; lizard; metapopulation theory; skink; thermal regime*

Introduction

Habitat loss and fragmentation are primary drivers of biodiversity loss worldwide (Fahrig 2003; Lindenmayer and Fischer 2006). In subalpine landscapes, substantial habitat loss and fragmentation occurs through the construction and expansion of ski resort infrastructure (WWF 2005). The expansion of ski resorts, and modifications undertaken within existing resort boundaries, are a concern as subalpine areas are sensitive but highly biodiverse environments that support many endemic species and communities (Martin 2013; Nagy and Grabherr 2009). Thus, significant disturbance to subalpine areas, coupled with the impacts of climate change (see Spehn et al. 2010; Whetton et al. 1996), may result in the loss of many species from these environments (WWF 2005).

Ski-related disturbances - chiefly associated with ski runs - have largely negative effects on wildlife (Laiolo and Rolando 2005; Negro et al. 2013; Sato et al. 2013a). Ski runs may be particularly detrimental landscape features for wildlife because structural complexity is extremely simplified in these areas. During the construction and annual maintenance of ski runs, native vegetation is cleared, rocks and logs are removed, and slopes are graded to create a smooth skiing surface (Behan 1983; Burt and Rice 2009; Hadley and Wilson 2004; Ries 1996). As a direct or indirect result of these changes, animals inhabiting or dispersing across disturbed ski areas are more susceptible to predation (Martin and Lopez 1999; Sato et al. 2014) and may have to travel greater distances than counterparts in undisturbed habitat to access food, shelter or thermoregulatory resources (Amo et al. 2007). Thus, the continuing creation, expansion, and maintenance of ski runs represent a considerable threat to subalpine reptiles by preventing individuals from dispersing freely throughout the landscape, impeding population connectivity and persistence. However, ski-run networks worldwide often incorporate small-to-large patches of relatively intact forest on, or between, ski runs (Hadley and Wilson 2004; JGR 2010; PBPL 2002; Strong et al. 2002). These vegetated patches may be capable of supporting populations of lizards (Bell and Donnelly 2006 and references therein), or alternatively, could be suitable

"stepping stones" (Bennett and Saunders 2010; Lindenmayer and Fischer 2006) allowing for movements of reptiles between otherwise disconnected areas of continuous forest in ski resorts. As far as we are aware, the value of these vegetated patches on ski runs for reptiles - or other wildlife - in disturbed subalpine landscapes has not been investigated.

In this paper, we use a detailed case study of a common, generalist reptile species -southern grass skink (*Pseudemoia entrecasteauxii*) - to test critical theories and predictions about the effects of habitat loss and fragmentation in a novel landscape context. Specifically, we investigated whether 1) forest loss; 2) patch size; 3) patch isolation; and 4) increased availability of edge habitat affect patterns of lizard abundance in a modified subalpine landscape.

First, we postulated that forest loss associated with ski run construction would have a negative effect on lizard abundance. Cleared habitats tend to support fewer lizards in a variety of ecosystem types (e.g., forests, D'Cruze and Kumar 2011; agricultural areas, Driscoll 2004; plantations, Fischer et al. 2005; subalpine environments, Sato et al. 2013b), and we expected to observe the same pattern in our study system (i.e., greatly reduced abundances of individuals in the cleared, grassy ski-run matrix compared to forested areas). Second, we postulated that large forested patches would support more lizards than smaller forested patches, which is an implicit assumption of metapopulation theory (Gaggiotti and Hanski 2004). This is because large patches offer a greater abundance of exploitable resources for lizards (assuming uniform habitat quality; Gaggiotti and Hanski 2004; Lindenmayer and Fischer 2006; Michael et al. 2008), and thus have a greater potential carrying capacity than small patches. Third, we postulated that isolated habitat patches on ski runs, far from continuous habitat, would support fewer lizards than less isolated patches. In Australia, lizards such as *P. entrecasteauxii* tend to be dispersal limited (tens of metres; see Clobert et al. 1994; James 1991) and also infrequently use ski runs (Sato et al. 2013b). Combined, these factors are likely to reduce rates of immigration of *P. entrecasteauxii* to isolated patches compared with less isolated patches (Moilanen and Hanski 1998), leading to local population size reductions and eventually localised population

extinctions (Eriksson et al. 2014). Finally, we postulated that lizards would be more abundant in edge habitats than the core of forested areas. The altered microclimatic conditions (e.g., increased light penetration that subsequently alters thermal regimes) available in edge habitats may benefit lizards (see Rubio and Simonetti 2011; Schlaepfer and Gavin 2001), encouraging increased use of these habitats. This is particularly the case for basking heliotherms such as *P. entrecasteauxii* (Green and Osborne 2012) that are constrained by highly variable environmental conditions at high elevations (Huang and Tu 2008).

In addition to addressing the four postulates above, we investigated a key potential driver, thermal regimes, which may contribute to the observed patterns of lizard distribution in subalpine ski resorts. Thermal regimes are an important determinant of reptile distribution worldwide (Diaz 1991; Huang et al. 2006) because sufficient warmth and solar radiation is required by these animals to assimilate energy for foraging and reproduction (Avery 1979; Martin et al. 2003). Previously, Sato et al. (2014) found that reduced structural complexity on ski runs can significantly alter thermal regimes, potentially influencing habitat selection and consequently the distribution of lizards. Based on those results, and given that structural complexity and insolation can vary dramatically across grass-forest ecotones (Burt and Rice 2009; Laiolo and Rolando 2005; Shine et al. 2002), we hypothesized that habitat fragmentation would alter the thermal regimes of matrix and patch habitats, and that lizard distribution patterns across these habitats would reflect avoidance of unfavourable thermal environments. Habitats that are too hot may present immediate risks to survival (Spellerberg 1972), and habitats that are too cold may limit opportunities for energy assimilation (Martin and Lopez 1999).

Methods

Study species and area

The most abundant lizard species detected in our study area, *P. entrecasteauxii*, occurs commonly in the Australian alpine-subalpine region (Green and Osborne 2012) but has a wider

distribution across south-eastern Australia (Wilson and Swan 2008). The species is a small (mean adult snout-vent length = 51.5 mm; mean adult mass = 3.0 g; C. Sato, unpublished data), diurnally-active heliotherm (Green and Osborne 2012) that can tolerate a wide range of body temperatures (T_{min} = 2.2-2.8°C, T_{max} = 41.9-42.5°C; Spellerberg 1972). The species occurs in a wide range of habitat types found in ski resorts, particularly where woody debris is plentiful (Michael and Lindenmayer 2010; Sato et al. 2013b), but tends to avoid highly modified ski runs covered with exotic grass (Sato et al. 2013b). While there is no specific information regarding the dispersal ability and home-range size of this species, studies investigating similar-sized lizards in Australia and elsewhere suggest dispersal capability is limited (<20 m; see James 1991; Melville and Swain 1999; Sumner et al. 2001) and home ranges are relatively small (<500 m^2; see Clobert et al. 1994; Olsson and Shine 2003; Turner et al. 1969).

We conducted surveys for *P. entrecasteauxii* at Thredbo ski resort (36°30′S 148°18′E; Fig. 1a) in Kosciuszko National Park, south-eastern Australia. In this region, during summer, the mean daily solar exposure ranges from 21.4 MJm^{-2} to 25.8 MJm^{-2} and the mean maximum temperature ranges from 19.1°C to 21.3°C (BOM 2014). During winter, the mean minimum temperatures range from -2.4°C to -3.8°C (BOM 2014). Annual precipitation is >2000 mm per year, with summers drier than winters (Green and Osborne 2012). The study area is covered with snow typically from mid-June to October.

We selected survey sites (n = 33) on south-facing slopes, varying in elevation from 1400 m to 1785 m. Across this range, vegetation communities in continuous forest and remnant native vegetation on ski runs intergrade from *Eucalyptus delegatensis-E. dalrympleana* (alpine ash-mountain gum) dominated forest on the lower slopes to *E. niphophila* (snow gum) dominated forests at higher altitudes. The understorey and ground layer of these sites vary in composition but generally have a dense cover including shrubs such as *Bossiaea foliosa* (leafy bossiaea), *Cassinia uncata* (sticky cassinia), *Hovea montana* (mountain hovea) and *Olearia phlogopappa* (dusty daisy-bush); herbs such as (*Acaena novaezelandiae* (bidgee widgee), *Asperula gunnii*

(mountain woodruff) and *Stellaria pungens* (prickly starwort); and grasses such as *Poa fawcettiae* (smooth blue snowgrass) and *Poa costiniana* (bog snow-grass); as well as considerable amounts of litter.

Field sites located in the centre of ski runs were dominated by exotic grasses, predominantly *Agrostis capillaris* (browntop bent) and *Festuca rubra* (red fescue). These sites all were subject to the same seasonal management practices (slashing and mowing during summer, and winter slope grooming).

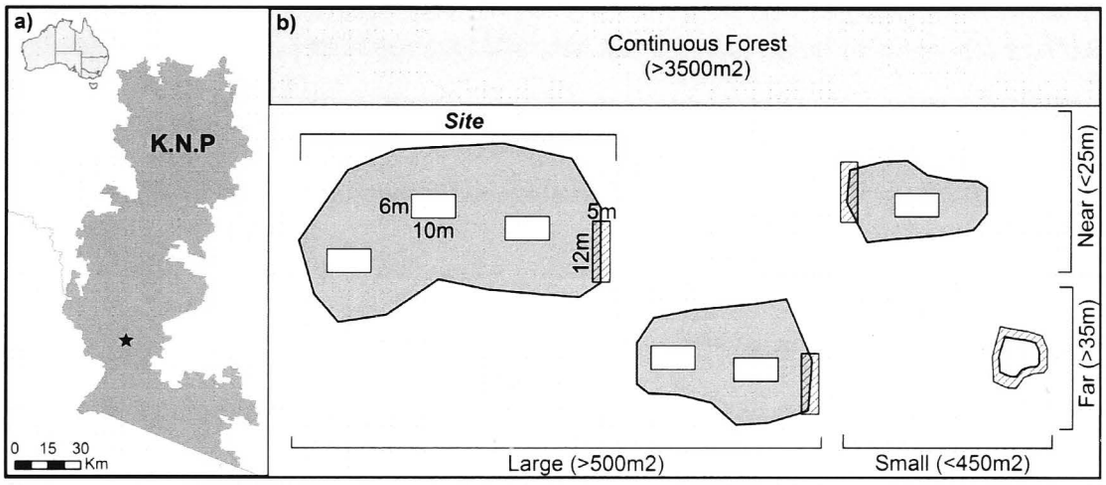

Figure 1. (a) Map of the study region within Kosciuszko National Park ("K.N.P"). The "★" represents Thredbo ski resort. (b) Schematic diagram of survey design for forested patches on ski runs. White boxes indicate core plots, hatched boxes indicate edge plots.

Sampling design and lizard surveys

To test our first hypothesis regarding effects of habitat type on lizard abundance, we conducted reptile surveys at a series of 'patch' sites (n = 19), 'control' sites (n = 7) and 'matrix' sites (n = 7) across the south facing slopes of Thredbo ski resort. We located 'patch' sites in forested remnants surrounded entirely by highly modified, exotic grass ski runs; 'control' sites in tracts of continuous, subalpine forest (>9 ha) showing minimal signs of disturbance; and 'matrix' sites in the centre of groomed ski runs cleared of native vegetation and rehabilitated with exotic grasses.

When selecting patch sites, we applied a strict set of criteria so that we could test the effects of size and isolation (i.e., Postulate 2 and Postulate 3) on lizard abundance. We chose patches according to two size classes: small (<450 m^2) or large (>500 m^2); and two isolation classes based on distance to large (>9 ha) tracts of minimally disturbed, subalpine forest: near (<25 m to forest) or isolated (>35 m to forest). We based these cut-offs for size and isolation on the natural history of lizards of similar body size (see James 1991; Melville and Swain 1999; Sumner et al. 2001; Turner et al. 1969). We also ensured sites were separated from one another by ≥20 m to maximise the chances that observations of lizards were independent. Using these selection criteria, we established five replicates of small, near patches; five replicates of small, isolated patches; five replicates of large, isolated patches; and four replicates of large, near patches. More replicates of large, near patches were unavailable because of limitations in the spatial availability of remnant vegetation meeting our criteria. Given the strict set of criteria we applied in selecting sites, the constraints of site availability were such that there was little scope for randomization of site selection.

Within each site (i.e., patch, control or matrix), we established a series of 6 x 10 m survey plots to standardise the area surveyed at each site (Fig 1b). For patch sites, we scaled the number of survey plots to the total size of the patch. Accordingly, we surveyed three plots in very large patches (>1600 m^2), two plots in large patches (540-1400 m^2), and one plot in small patches (290-420 m^2). We located plots in these patches ≥5 m from the edge of the nearest ski run and ≥10 m from one another, along a transect that roughly bisected the patch (Fig. 1). For very small patches (<90 m^2), we surveyed the entire area. Control and matrix sites far exceeded the size of our largest patch (i.e. >3500 m^2), so we established the maximum number of survey plots (n = 3) in these areas, ensuring that they were separated from one another by ≥10 m.

Finally, to test our fourth postulate regarding the effect of edge availability on lizard abundance, we surveyed edge habitats at each patch site. The edge between the vegetated patches and surrounding exotic grass matrix was hard (*sensu* Forman 1995; see Appendix 1) and

microhabitat conditions differed noticeably between forest and exotic-grass ski run (C. Sato, personal observation). We defined edge habitat as the area extending 2 m into a patch and 3 m into the exotic-grass ski run (Fig. 1b). We used this 'definition' of an edge based on observations of differences in abiotic characteristics; light penetration decreased markedly within 2 m of the edge of a patch, and beyond this appeared less variable. This edge definition also allowed us to maximise consistency in the size of plot surveyed between edge habitats and core habitats. Thus, at each patch site, we surveyed one edge plot (5 x 12 m), unless islands were very small (<90 m^2), in which case we surveyed the entire edge habitat around the patch.

We conducted reptile surveys during three periods (10 January - 6 February 2011, 10 February - 11 March 2012, and 29 November 2012 - 20 January 2013). At each survey plot, we conducted non-destructive, time- and area-constrained (10 min/60 m^2) active searches (a standard survey technique for diurnally active, terrestrial heliotherms; Manning et al. 2013; Michael et al. 2012; Sato et al. 2013b). This method involved systematically moving through a plot searching for lizards around vegetation, rocks, logs, and litter. We recorded all observations of lizards during 10-minute survey periods. At each plot, we completed nine repeat surveys across three survey periods (i.e., three days per survey period, and three survey periods across two field seasons, thus a total of 90 minutes at each site). To maximise chances of detecting lizards, we conducted surveys only on calm, partly sunny to sunny days. Moreover, we randomised the timing of visits to sites to survey 'morning' (0730-1200; Australian Eastern Standard Time [AEST]) and 'afternoon' (1200-1600 AEST) periods to avoid detectability issues associated with temporal variation in lizard numbers.

Thermal environments

To investigate the effects of habitat fragmentation on thermal regimes, and the effects of thermal environment on lizard distribution patterns, we used temperature loggers (Thermochron i-Buttons, Thermodata Pty Ltd, QLD, Australia; diameter, 17.4 mm; height, 5.9 mm) to record

ground surface temperatures. At each plot within 'isolated' patches, we deployed two temperature loggers - one on the eastern side of the plot and one on the western side of the plot - to capture the spatial variation in ground surface temperatures available to lizards over their active period (see Tracy and Christian 1986). For edge plots, we placed two temperature loggers at the interface between the vegetated patch and exotic grass matrix. For control and matrix sites, we placed two temperature loggers in the central plot – one on the eastern side and one on the western side. We ensured that all loggers were in contact with the ground (secured in place with a tent peg) and partially covered by grasses or litter to prevent exposure to lengthy periods of direct sunlight.

We programmed all loggers to record temperature every 30 minutes and left the loggers *in situ* from 1 December to 31 December 2012 – the month of our field season representing median long-term average temperatures for the study area (BOM 2014). After this time, we collected all loggers for analysis.

Statistical analysis

To explore the effects of fragmentation on the number of lizards observed, we fitted Hierarchical Generalised Linear Models (HGLMs; Lee et al. 2006) assuming a quasi-Poisson distribution with a log link function for the response and a gamma distribution with a log link function for the random component. We fitted two models for lizard observations. We included the number of lizards observed per survey period as the response variable, and 'Plot' nested within 'Site' as random effects. Additionally, in both models we included 'Survey Period' as a fixed effect, to determine whether the numbers of lizards observed differed between survey periods. We focused our first model on the effect of disturbance (i.e., habitat loss) on the number of lizard observations (Postulate 1), including 'Habitat Type' (i.e., matrix, patch or control) as a fixed effect. We then excluded matrix sites from further analyses of lizard observations because we detected few individuals in the matrix ($n = 6$ individuals across all sites and surveys), and the inclusion of these sites in the HGLMs masked the effects of other

variables of interest (e.g., patch size and patch isolation). For the second HGLM, we used the three habitat fragmentation attributes identified in our hypotheses as fixed effects: patch size, patch isolation and edge effects ('Forest Location') (Postulates 2 - 4). Arguably, differing densities of lizards observed in edge and core habitats of patches could be due to the increased difficulty in detecting lizards in densely vegetated core areas compared with comparatively more open edge habitats. Thus, to determine whether rates of detection differed between edge and core habitats, we fitted N-mixture models for abundance (Royle 2004) assuming a Poisson distribution for the latent abundance using 'unmarked' package (Fiske and Chandler 2011) implemented in R (R Core Team 2013).

To analyse temperature data, we included temperature readings taken between 0500 and 1830 from all sites, when lizards were likely to be active. For these readings, we calculated the mean, absolute maximum, absolute minimum, and range of ground surface temperatures recorded at each data logger over the 31-day period that loggers were deployed. We then used linear mixed models (Harville 1977) to determine whether there were significant differences in the thermal environments of sites. We included 'Habitat Type', 'Patch Size', and 'Forest Location' (i.e., edge vs. core habitat) as fixed effects, and 'Logger Position' (i.e., eastern or western side of plot) and 'Plot' nested within 'Site' as random effects to account for spatial correlation. We included temperature measures (mean, absolute maximum, absolute minimum, and range of ground surface temperatures) as the response variables.

For temperature data, we also investigated the length of time that ground surface temperatures fell outside the critical body temperature thresholds of *P. entrecasteauxii* (an absolute critical minimum of 2.2°C and an absolute critical maximum of 42.5°C; see Spellerberg 1972). Beyond these temperature limits, lizard locomotion is impaired, and consequently individuals lose the ability to escape from conditions that may lead to their death (Spellerberg 1972). Lizards exposed to ground surface temperatures outside their critical thermal thresholds for more than a

few minutes cannot forage for food, escape predation attempts, or endure physiological stresses (Spellerberg 1972).

In summary, we quantified the total number of hours that ground surface temperatures exceeded the absolute critical maximum body temperature, and fell below the absolute critical minimum body temperature, of *P. entrecasteauxii* as a proportion of the total number of hours available for lizard activity (434 hours across 31 days). We then fitted a quasi-binomial HGLM to investigate whether the calculated proportion of hours differed between 'Habitat Types' (i.e., matrix, patch and control), which was a fixed effect. To account for the spatial structure, we included 'Plot' nested within 'Site' as random effects. We used GenStat 16 (VSN International Ltd) for all statistical computation.

Results

Effects of fragmentation

Across the three survey periods, we recorded 543 *P. entrecasteauxii* observations. We detected most of these individuals in patches ($n = 365$) and undisturbed forest ($n = 172$). We observed few *P. entrecasteauxii* in the matrix (i.e., centre of ski runs; $n = 6$). There was no difference in the number of lizards observed between survey periods ($\chi^2_2 = 2.395$, $P = 0.302$).

The number of *P. entrecasteauxii* observations differed between habitat types ($\chi^2_2 = 30.38$, $P < 0.001$; Fig. 2a), with fewer *P. entrecasteauxii* recorded in the matrix. After we excluded matrix sites from the analysis, we found that patch size did not influence the number of lizards observed ($\chi^2_1 = 2.806$, $P = 0.246$), but that forest location did. More lizards were observed in edge plots than core plots ($\chi^2_1 = 38.55$, $P < 0.001$), and more lizards were observed in the edges of vegetated patches near continuous forest than in the edges of patches far from continuous forest, or in the core of any site ($\chi^2_1 = 4.105$, $P = 0.04$; Fig. 2b). We found no difference in detection rates of lizards between edge and core habitats (P=0.45).

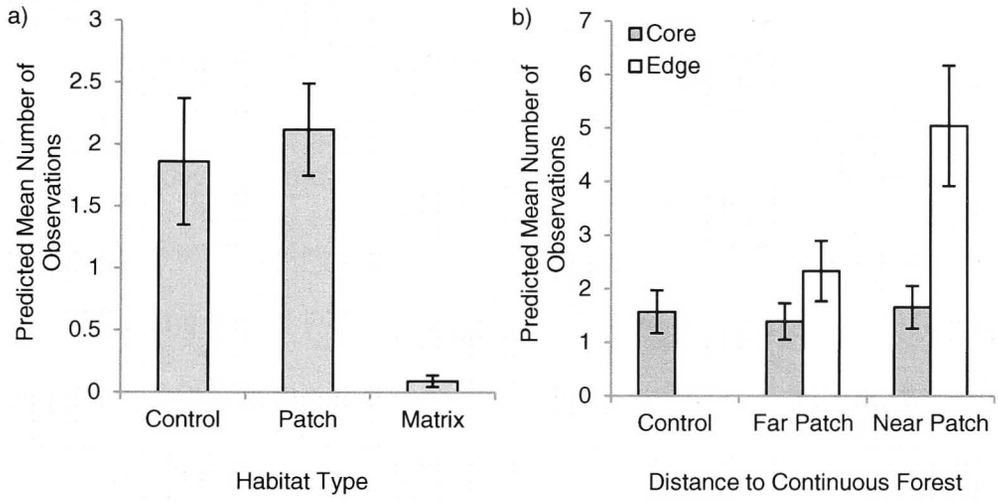

Figure 2. Predicted mean number of *P. entrecasteauxii* observations (± SE) in: (a) three habitat types: control, patch and matrix; and (b) the edge and core of near patches, far patches and the core of undisturbed forest (controls). All predictions are given on the natural scale.

Thermal environments

We found an interaction between Habitat Type and Forest Location (i.e., edge vs. core habitat) for all measures of ground surface temperature (mean, maximum, minimum, and range; $P < 0.001$ for all measures; Table 1). Matrix sites had higher mean, maximum and range of ground surface temperatures than the edge or core of patches, or controls ($P < 0.001$ for all measures; Table 1). Additionally, the edges of patches had higher mean, maximum and range of ground temperatures compared with core habitats (Table 1). Conversely, matrix sites had lower minimum ground surface temperatures compared to patches or controls ($P < 0.001$; Table 1).

Table 1. Mean, maximum, minimum and range of temperatures recorded (with average standard errors of differences; 'S.E.D') in the matrix (M), edges of patches (EP), core of patches (CP) and controls (F).

	TEMPERATURE MEASURE (°C)			
	Mean	Maximum	Minimum	Range
PLOT TYPE				
M	22.4	37.6	5.4	32.2
EP	17.4	31.8	6.2	25.6
CP	13.8	21.0	6.7	14.3
F	14.5	24.0	6.4	17.7
S.E.D	0.70	1.93	0.36	1.96
WALD STATISTIC	$\chi^2_1 = 76.80$*	$\chi^2_1 = 66.32$*	$\chi^2_1 = 21.54$*	$\chi^2_1 = 71.49$*

Wald statistic provided for interaction between *Habitat Type* and *Forest Location* (Location).
*$P<0.001$.

The length of time that ground temperatures exceeded the critical maximum body temperatures of lizards (42.5°C; see Spellerberg 1972) also varied with Habitat Type and Forest Location. Matrix sites had longer periods when ground surface temperatures exceeded the critical maximum body temperatures of lizards compared with either patches or controls (matrix: 0.74 ± 0.21h day^{-1}; patch: 0.17 ± 0.07h day^{-1}; control: 0.03 ± 0.02h day^{-1}; $\chi_2^2 = 20.28$, $P < 0.001$; Fig. 3a,c). In terms of edge effects, the ground surface temperature of edge plots exceeded the critical maximum body temperature of lizards for longer periods than core plots, but not as long a period as matrix sites (edge: 0.44 ± 0.16h day^{-1}, core: 0.01 ± 0.01h day^{-1}, matrix: 0.74 ± 0.21h day^{-1}; $\chi_1^2 = 5.81$, $P = 0.016$; Fig. 3b).

The length of time that ground temperatures fell below the critical minimum body temperatures of lizards (2.2°C; see Spellerberg 1972) did not differ among Habitat Type ($\chi_2^2 = 0.8849$, $P = 0.642$) or Forest Location ($\chi_1^2 = 0.4796$, $P = 0.489$).

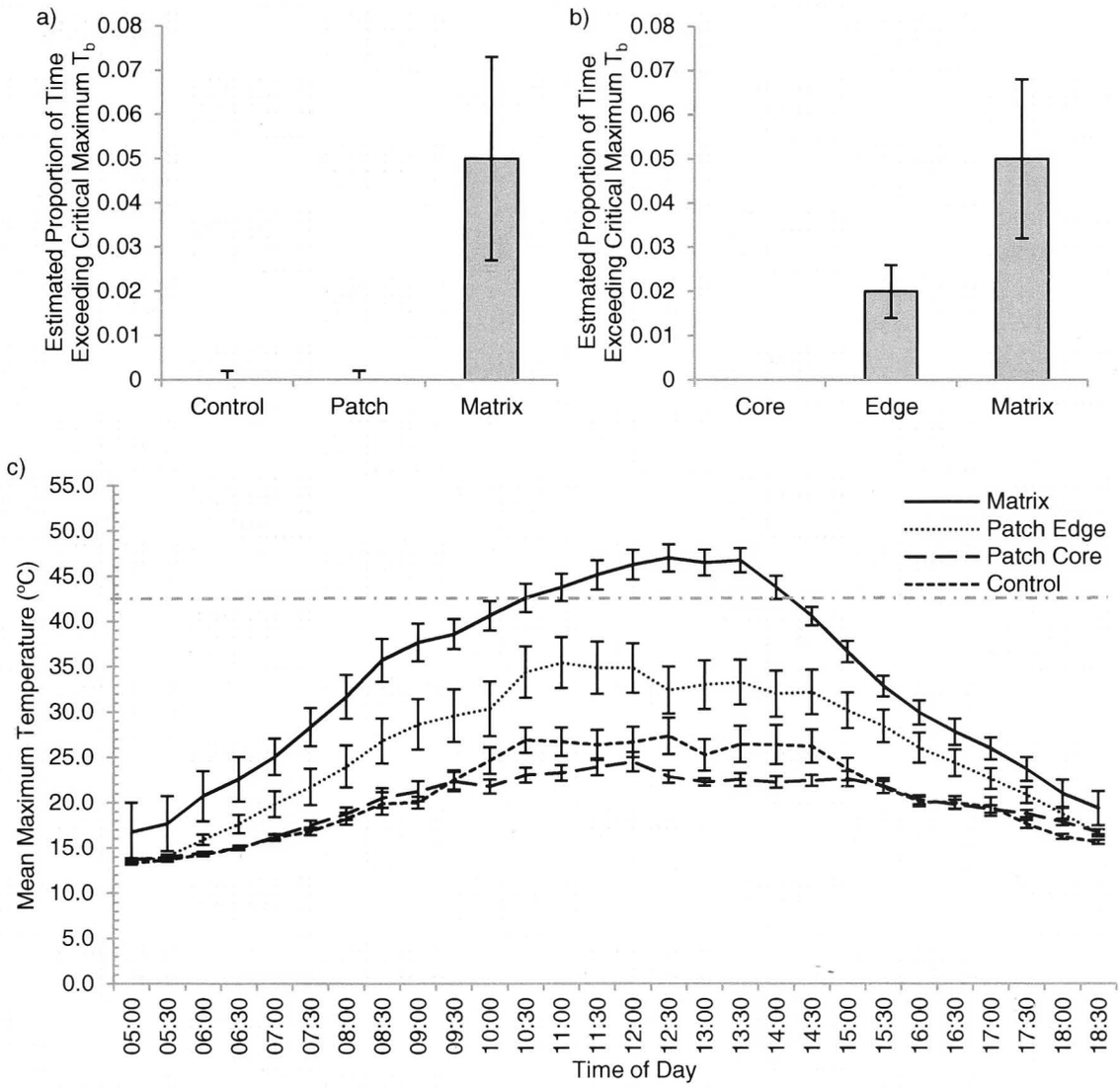

Figure 3. Predicted mean proportion of time (±SE) that ground surface temperatures exceeded the critical maximum body temperature (T_b) of lizards in three habitat types: (a) control, patch and matrix; and (b) core habitat, edge habitat and matrix; (c) Mean (±SE) absolute maximum ground surface temperatures (°C) recorded in matrix sites, patches (edge and core), and controls across 31 days, during lizard activity periods. The 'time of day' is reported as Australian Eastern Standard Time. The dashed horizontal line represents the absolute critical maximum body temperature of *P. entrecasteauxii* recorded by Spellerberg (1972).

Discussion

Despite the considerable threat that habitat degradation poses to reptile populations (Todd et al. 2010), research investigating effects of ski run construction on reptiles has been limited (Sato et al. 2013a), particularly regarding how fragmentation affects reptile distributions and whether this may be driven by alterations to thermal environments. We found that both thermal environments and lizard abundance were affected by fragmentation. Maximum and mean ground temperatures were higher in the matrix (i.e., the centre of exotic grass ski runs), and exceeded the critical maximum body temperature of lizards for longer periods, than in forested areas (patches or controls). Similarly, edge habitats were warmer than core habitats of forested areas. Observations of lizards appeared to correspond with these thermal gradients; we observed lizards infrequently in the matrix, but recorded them in remnant forested patches on ski-run networks (supporting Postulate 1). We detected more lizards at the edges of patches near controls (i.e., continuous forest) than at the edges of patches far from controls, or in the core of any forested area (supporting Postulate 3 and substantiating Postulate 4). Patch size did not appear to influence lizard abundance (refuting Postulate 2).

Based on our findings, we argue that the creation of ski runs, through the removal of large tracts of native vegetation and structural habitat features, has a negative effect on lizard distributions (see also Sato et al. 2013b). This effect is likely due to the limited structural complexity available on ski runs, which in turn limits available resources for basking, shelter from predators, or refugia from extreme ground surface temperatures (Sato et al. 2014; Fig. 3). Without these resources, the immediate and long-term survival of lizards in these areas could be greatly reduced. However, retaining remnant patches on these ski runs may, in part, mitigate the negative effects of habitat loss on lizard populations. Regardless of patch size, remnant patches are capable of supporting lizards in similar densities to undisturbed forest (Fig. 2). Thus, remnant patches are important design features in ski resorts that may facilitate the persistence of lizards in modified subalpine landscapes.

One reason for the similarities in lizard densities between undisturbed forest and remnant vegetation patches is the increased availability of edge habitat for lizards occupying remnant patches. Edge habitats provide benefits to fragmented lizard populations through altered microclimates (e.g., increased sunlight, decreased humidity, higher temperatures; see Collinge 1996). The altered microclimatic conditions allow lizards at high elevations to maximise thermoregulatory opportunities and energy assimilation (Angilletta 2001; Huang et al. 2013) in an environment where conditions are extreme and highly variable (Carrascal and Diaz 1989; Huang and Tu 2008). Our results strongly suggest that lizards may be selecting edge habitats over all other available habitats; it was in the edges of remnant patches where we observed the highest number of *P. entrecasteauxii* across all habitat types (Fig. 2). This selection is likely due to the optimal thermal qualities of these environments. Edges are warmer than core habitats but cooler than exotic grass ski runs, providing lizards with increased thermoregulatory opportunities.

Edges also may provide preferred habitat for lizards because, in addition to improved thermal conditions, refuges from predators are close to basking sites. The proximity of refuges may increase the probability of escaping a predator (Greene 1988; Martin and Lopez 1999), and also can result in improved body condition (and consequently fitness) when compared with conspecifics that travel greater distances to find shelter (Amo et al. 2007). Thus, the combination of favourable thermal regimes and proximity to shelter sites provided by vegetated patches on ski runs could offer lizards suitable environments for extended periods of 'risk-minimised' basking. While we did not quantify the influence of interacting factors such as predation risk and structural complexity on lizard habitat choices, this would be an interesting avenue of future research that could further explain the patterns of lizard distribution in subalpine environments affected by ski resort developments.

Despite the benefits derived from edge habitats in remnant patches, the degree to which edges of remnant patches, and the remnant patches themselves, can mitigate the negative effects of initial habitat loss on lizard populations is likely to be highly dependent upon the isolation of those patches. Patch isolation is likely to influence the abundance and ultimately the probability of local population extinction of reptiles. This is because the matrix remains largely unused by lizards due to a combination of extreme thermal conditions and increased rates of predation (Sato et al. 2014). Hence, as vegetated patches become more isolated from continuous forest (i.e., as individual ski runs are widened or entire ski-run networks are expanded), it is likely that dispersal will be restricted or potentially prohibited altogether, as in other ecosystems (Dixo and Metzger 2009; Munguia-Vega et al. 2013). The further lizards must travel across inhospitable, exotic grass ski runs to reach vegetated patches, the more likely they will be preyed upon (Sato et al. 2014), suffer from heat stress due to extreme thermal conditions (Spellerberg 1972), or progressively lose body condition if multiple movements occur across a season (Amo et al. 2007). As a consequence, rates of immigration and colonization to more isolated patches will be reduced, preventing boosts to local populations and increasing extinction risk (Gaggiotti and Hanski 2004). While lizards were not absent from isolated patches in our study, the abundance of lizards was reduced in these areas, even in the edge habitats of these patches, compared with less isolated patches. Hence, lizards may be unwilling or incapable of frequently crossing ski runs.

Implications for management

First and foremost, we argue that it is essential, wherever possible, to retain undisturbed native vegetation and other elements of structural complexity (such as rocks and logs) to facilitate the persistence of lizards in disturbed subalpine environments. However, retention of structural complexity on ski runs often directly compromises the safety of skiers and snowboarders (Kelsall and Finch 1996), so it is not always possible to conserve structural complexity. In such cases, we contend that careful design and management of ski runs, in a way that decreases isolation of suitable habitat patches, will assist the continued dispersal of lizards between habitat

patches, thus reducing landscape-scale extinction risk. The distances between vegetated patches on ski runs and continuous forest can be minimised in several ways. First, for narrow ski runs (<20 m), buffering the edges of runs with native vegetation (e.g., low heath species that are unlikely to impede skier activity) will reduce the width of the exotic grass matrix. Heath vegetation should provide sufficient structural complexity to attenuate extreme ground surface temperatures, and potentially provide sufficient cover to reduce rates of predation on lizards crossing ski runs (Sato et al. 2014). Second, for wide exotic grass ski runs (>40 m), the distances between forested areas could be minimised through planting patches of native forest species on the runs (in addition to buffering ski run edges with native vegetation). Such plantings would break up the extent of the exotic grass matrix, potentially allowing lizards to inhabit the new patches, or to use them as 'stepping stones' to larger patches of forest (Bennett and Saunders 2010; Lindenmayer and Fischer 2006). Finally, connections between suitable habitat patches could be restored by re-introducing structural habitat features onto ski runs such as semi-submerged rocks or timber, similar in design to the wildlife crossings used for the threatened *Burramys parvus* (mountain pygmy possum; Mansergh and Scotts 1989), which may need to be relocated before each winter. However, the efficacy of wildlife crossings for reptiles needs to be investigated before broad-scale implementation across ski resorts.

Acknowledgements

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Appendix 1. Example of a vegetated patch with hard edges on an exotic grass ski run at Thredbo ski resort.

PAPER V: Managing ski resorts to improve biodiversity conservation: Australian reptiles as a case study.

Paper V is intended as a summary and concluding chapter for the thesis, but also a management report that can be used by practitioners to improve conservation outcomes for reptiles in Australian ski resorts. In this paper, I draw together current knowledge on the effects of ski-related disturbances on reptiles, including all the findings from my thesis research. Based on this information, I recommend management strategies to facilitate the persistence of reptiles in Australian ski resorts.

Sato, C.F., Schroder, M., Green, K., Michael, D.R., Osborne, W.S. & Lindenmayer, D.B. (2014) Managing ski resorts to improve biodiversity conservation: Australian reptiles as a case study. Ecological Management & Restoration 15: 147-152.

Summary

Alpine/subalpine environments are diverse systems that support many endemic species. Worldwide, these ecosystems are under threat from ski resort disturbances – even in areas broadly designated for biodiversity conservation. The effects of ski resorts on reptiles are largely unknown, making it difficult to implement effective conservation actions. Many ski resorts do not currently address the needs of reptiles, even those listed as threatened, in their management plans. If reptiles are to continue inhabiting ski resorts in Australia, strategies must be implemented that target their conservation. To begin to address this problem, we summarise current research investigating the effects of ski resorts on reptiles. Based on this information, we recommend strategies that will enhance the conservation of reptiles in areas affected by ski-related disturbances. Suggested strategies include (i) restricting intensive disturbances to already highly modified areas of Australian ski resorts, (ii) avoiding disturbance of remaining native vegetation and structural complexity in ski resorts and (iii) re-establishing structural complexity at highly modified sites through revegetation programs, or through the cessation of mowing during peak reptile activity periods. While these strategies are designed to facilitate the persistence of reptiles in ski resorts, their long-term success can only be evaluated by monitoring their effectiveness.

Keywords: *habitat fragmentation; lizards; matrix; patch; ski run; thermal regime*

Introduction

Alpine and subalpine ecosystems occupy a relatively small proportion of the Earth's terrestrial landmass (approximately 7.9% excluding Antarctica; Körner *et al.* 2011), and are particularly limited in Australia (approximately 0.15% of terrestrial Australia; Williams & Costin 1994). Nevertheless, alpine/subalpine areas are biodiverse and support many endemic species (DEC 2006; Nagy & Grabherr 2009). These environments are also economically-significant tourist destinations, due to the winter recreation opportunities they offer (e.g. the combined benefit of Australian alpine resorts to total gross state product was AUD$1.561 billion in 2011; ARCC 2012). As a result of the construction of ski-related infrastructure, ecological communities in alpine/subalpine areas are affected by habitat loss and fragmentation. Moreover, these areas are likely to face continued vegetation disturbance and habitat modification with the increasing use of ski resorts for summer activities including downhill mountain biking (Pickering *et al.* 2003; Needham *et al.* 2004).

The majority of Australia's ski-related infrastructure is confined to the Australian Alps on the mainland (ARCC 2012). The Australian Alps cover 1.6 million hectares and encompass most of the alpine and subalpine areas on mainland Australia within a series of interconnected Protected Areas (Coyne 2001) (Fig. 1). Because major ski operations are located within the bounds of national parks in New South Wales ('NSW' hereafter) or are surrounded by national parks in Victoria (Morrison & Pickering 2013) (Fig. 1), it is important to understand the extent of ski-related impacts in alpine/subalpine Australia.

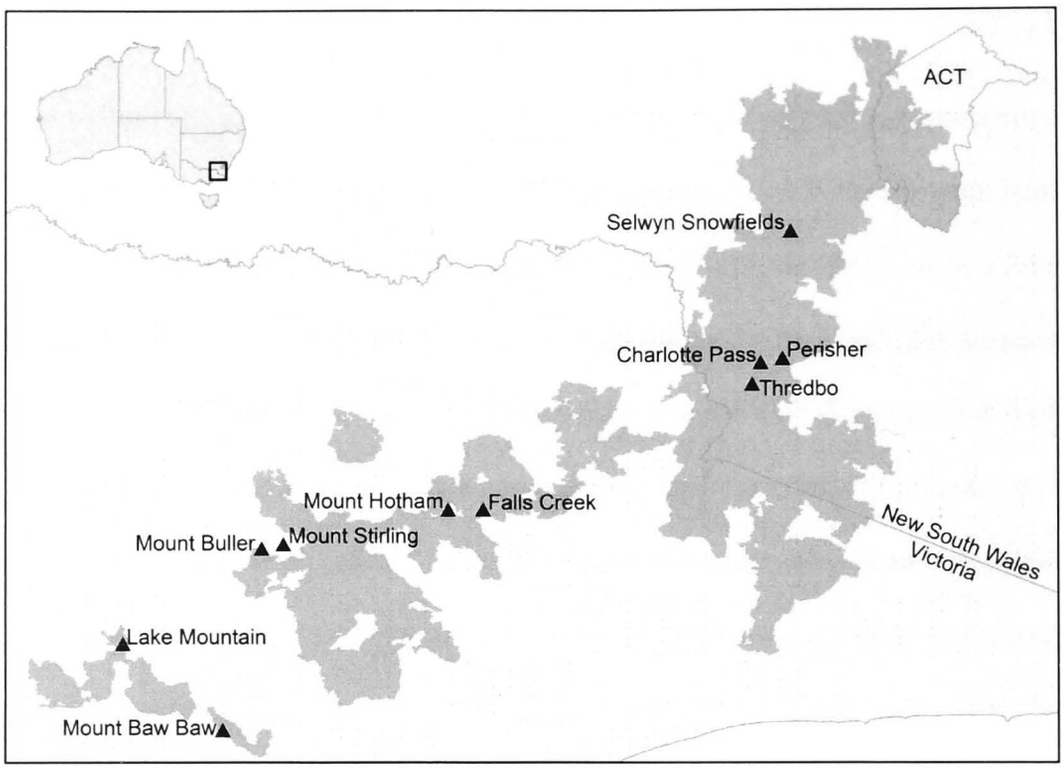

Figure 1. Map of Australian ski resorts and land conserved within protected areas across the mainland Australian Alps. Black triangles represent ski resorts, and dark grey shading indicates land designated as a protected area. 'ACT' stands for Australian Capital Territory.

The national parks system in Australia protects and conserves biodiversity while maintaining sustainable visitor use (DEC 2006). Hence, to achieve these sometimes conflicting objectives, all new ski developments are conducted under strict state and Australian Government legislative, planning and management frameworks (Table 1). If a proposed ski-related development poses a risk to the persistence of a threatened species or community, the applicable legislation depends upon whether the affected species or community is listed under state or national legislation. In some instances, species or communities are listed at both legislative levels (e.g. Alpine She-Oak Skink *Cyclodomorphus praealtus,* DoE 2014), and all legislation, policies and plans must be satisfied (e.g. minimising risk to threatened species) before developments take place. Essentially, these acts, policies and plans have been designed to facilitate environmentally-sensitive development of alpine/subalpine areas (DEC 2006). This is partially because, of the 160 state and nationally listed threatened plant and animals species located across the entire Australian Alps (Coyne 2001), threatened endemic species that are restricted to a small subset of alpine-subalpine habitats inhabit areas within the footprint of ski resorts (including the Alpine She-Oak Skink and the Guthega Skink *Liopholis guthega*; Fig. 2).

Further disturbance to their habitats could substantially reduce their survival in these areas (see TSSC 2009; TSSC 2011).

Figure 2. Two lizard species listed as endangered under the Environmental Protection and Biodiversity Conservation Act (1999) and restricted to elevations above 1500 m in the Australian Alps. (a) Alpine She-Oak Skink; (b) Guthega Skink. Photos by C. Sato and D. Michael.

The legislative framework currently in place to protect alpine environments may support the conservation of well-studied threatened species such as the Mountain Pygmy Possum (*Burramys parvus*) because improved understanding increases our capacity to effectively manage species and ecosystems (Christensen *et al.* 1996). However, for species with limited, or no information concerning their basic ecology or sensitivity to ski-related disturbances, legislative frameworks guiding management may not achieve conservation outcomes. This is the case for alpine/subalpine reptiles – a relatively diverse cold-climate assemblage that is comprised of many endemic species (Green & Osborne 2012), of which two species (Alpine She-Oak Skink and Guthega Skink) are listed as nationally endangered under Australian Government legislation. For both species, ski-related disturbances are identified as a significant threat (TSSC 2009; TSSC 2011). However, few empirical studies have investigated the impacts of ski-related disturbances on these rare species, or indeed other, more common reptile species (Sato *et al.* 2013a; Sato *et al.* 2014).

Table 1. A summary of characteristics of ski resorts on mainland Australia, as well as the legislative frameworks governing those resorts in regards to developments in the alpine-subalpine zone.

Ski Resort	Skiable Area (ha)[a]	Visitation in 2011 (Visitor Days[b])[a]	Australian Government Legislation	State Legislation, Policies and Plans
New South Wales				
Perisher Range	1245		*Environmental Protection and Biodiversity Conservation Act 1999*	*National Parks and Wildlife Act 1974* *Threatened Species Conservation Act 1995* *State Environmental Planning Policy (Kosciuszko National Park – Alpine Resorts) 2007* *Kosciuszko National Park Plan of Management 2006*
Thredbo	480			
Charlotte Pass	50			
Selwyn Snowfields	45			
Total	1,820	1,654,788[c]		
Victoria				
Lake Mountain	590	105,688	*Environmental Protection and Biodiversity Conservation Act 1999*	*Planning and Environment Act 1987* *Conservation Forests and Lands Act 1987* *Environmental Protection Act 1970* *Flora and Fauna Guarantee Act 1988* *Wildlife Act 1975* *Wildlife Act (Regulations) 2002* *Permitted clearing of native vegetation - Biodiversity assessment guidelines* *Victoria's Biodiversity Strategy (1997)* *Alpine Resorts Strategic Plan 2012* *Alpine Resorts Planning Scheme*
Falls Creek	450	386,510		
Mt Hotham	300	455,154		
Mt Buller	263	472,575		
Mt Baw Baw	37	74,793		
Mt Stirling	0[d]	7,025		
Total	1,640	1,501,745		

[a] Data obtained from ARCC (2012) for Visitation in 2011, and ARCC (2013) for skiable area.

[b] Visitor Days = visitors x length of stay

[c] No breakdown by resort available for New South Wales

[d] Mt Stirling Ski Resort has ~65 km of cross-country ski trails, of which 35km are groomed

In this paper, we draw together recent research investigating the effects of ski-related disturbances on reptile distribution and identify the potential drivers that contribute to the patterns observed. Based on this information, we suggest management actions that can be implemented to improve conservation outcomes for reptiles inhabiting areas affected by ski-related disturbances, as well as potential factors that may influence the success of those actions.

Environmental Disturbances Arising From Ski Resort Developments

The construction, expansion and maintenance of ski resort infrastructure can involve extensive and ongoing disturbance to alpine/subalpine ecosystems. Beyond outright loss of habitat caused by the construction of ski resorts and related infrastructure (most of which has already occurred), arguably the most detrimental ski-related disturbance is the construction of groomed ski runs (Wipf *et al.* 2005; Caprio *et al.* 2011; Fig. 3). Groomed ski runs are the parts of ski resorts where habitat structural complexity is simplified and the original, native vegetation composition is substantially altered. Modification involves the removal of large swathes of vegetation as well as rocks, logs or other debris (Ries 1996; PBPL 2002). Bare slopes are then stabilised using exotic grasses (Tsuyuzaki 1994). Ongoing maintenance involves slope grooming during winter, as well as rock or tree removal and vegetation slashing during summer (PBPL 2002; Kubota & Shimano 2010). Earthworks also may be undertaken to eliminate natural humps or hollows occurring on a ski run to improve skier safety (PBPL 2002). Comparable environmental effects may be observed for structures such as half-pipes, particularly those of international competition standard, that require similar construction and maintenance practices to groomed ski runs (e.g. earthworks and winter snow grooming, FIS 2008).

Figure 3. Example of a groomed ski run at Thredbo Ski Resort in New South Wales, where native vegetation, rocks and logs have been removed, and bare slopes are stabilised using exotic grasses including Browntop Bent and Red Fescue.

Effects of Ski-Related Disturbances on Reptiles

Worldwide, the effects of ski-related disturbances generally are detrimental to wildlife, including reduced richness, diversity and abundance of animals observed in areas affected by ski resorts (Sato *et al.* 2013a). For reptiles, Sato *et al.* (2013a) found only two peer-reviewed studies investigating the effects of ski-related disturbances on biodiversity (Shine *et al.* 2002; Amo *et al.* 2007) and different conclusions were reached from those studies. Amo *et al.* (2007) suggested that ski runs have negative effects on reptile body condition over time, whereas Shine *et al.* (2002) indicated that the type of clearing undertaken to create ski runs has the potential to alter thermal regimes in ways that benefit some oviparous reptiles.

More recently, research at three Australian ski resorts (Perisher, Charlotte Pass and Thredbo, in NSW) identified negative effects of ski-related disturbances on reptiles (Sato *et al.* 2014). The research showed that:

1) Disturbed habitats support fewer specialist lizards (i.e. Alpine She-Oak Skink, Guthega Skink, and Tussock Skink, *Pseudemoia pagenstecheri*) than undisturbed habitats. Generalist lizards (e.g. Southern Grass Skink, *Pseudemoia entrecasteauxii*) appear more resilient to

disturbance, occurring frequently in disturbed heathlands and woodlands (Sato *et al.* 2013b).

2) All lizard species tend to avoid ski runs dominated by exotic grasses. The Alpine She-Oak Skink, Guthega Skink, Tussock Skink and Southern Grass Skink prefer more structurally complex habitats, such as heathlands, woodlands and undisturbed native grasslands (Sato *et al.* 2013b);
3) Lizards use patches of remnant vegetation retained on or between ski runs (Sato *et al.* 2013b; Sato *et al.*, *in review*, 2014).
4) The size of a remnant patch of native vegetation does not influence lizard density, whereas the proximity of patches to continuous forest does. Patches close to continuous forest (<20 m) support higher densities of lizards than patches far from (>30 m) continuous forest (Sato *et al.*, *in review*, 2014);
5) In remnant patches, lizard densities are higher in edge habitats than core habitats (Sato *et al.*, *in review*, 2014).

Factors Driving Observed Reptile Patterns

To improve the efficacy of management actions aimed at conserving biodiversity, an understanding of distribution patterns, as well as the processes driving those patterns, is required (Christensen *et al.* 1996). In Australian ski resorts, four key drivers contribute to patterns of reptile distributions: (i) vegetation composition, (ii) habitat structural complexity, (iii) predation risk and (iv) thermal regimes (Sato *et al.* 2014; Sato *et al.*, *in review*, 2014).

Vegetation Composition

Vegetation composition, particularly the dominance of exotic plant species, can influence reptile richness and abundance (reviewed by Martin & Murray 2011). In subalpine areas Sato *et al.* (2013b) found that lizard abundance was related to one or more native plant species associated with distinctive Australian alpine-subalpine vegetation formations (Table 2). No lizard species

was positively associated with exotic plants (Table 2). In fact, in areas where exotic grass coverage was high, few lizards were detected (Sato *et al.* 2013b). Thus, relationships between reptiles and vegetation composition highlight the importance of preserving native vegetation in ski resorts – particularly rocky heathlands and sod-tussock grasslands for threatened species such as the Alpine She-Oak Skink and Guthega Skink – as well as the prevention of activities that facilitate the proliferation of exotic plant species (e.g. seeding ski slopes using exotic grasses after initial construction).

Table 2. Relationships of four species of Australian subalpine reptile with vegetation and structural habitat attributes.

Species	Relationships with Vegetation	Relationships with Structural Complexity	Associated Australian Alpine-Subalpine Formation
Alpine She-Oak Skink	+ Spreading Rope-rush (*Empodisma minus*) + native grass (*Poa* sp.) cover	- logs - total vegetation cover*	Sod-tussock grassland
Guthega Skink	+ Alpine Mint-bush (*Prostanthera cuneata*) + Ovate Phebalium (*Nematolepis ovatifolia*)	+ large rocks (>5 m^3) + total vegetation cover*	Rock boulder heath
Southern Grass Skink	+ Snow Gum (*Eucalyptus niphophila*) + Alpine Daisy Bush (*Olearia phlogopappa*) + Dusty Daisy Bush (*Olearia brevipedunculata*)	+ woody debris	Snow gum woodland
Tussock Skink	+ Spreading Rope-rush (*E. minus*) - exotic grass cover (Browntop Bent [*Agrostis capillaris*], Red Fescue [*Festuca rubra*])	- understorey shrub cover	Sod-tussock grassland

* combined cover of vegetation from the ground, understorey and canopy strata; "+" indicates a positive relationship; "-" indicates a negative relationship. Relationships obtained from Sato *et al.* (2013b). Associated alpine/subalpine formations obtained from Costin *et al.* (2000).

Structural Complexity

Groomed ski runs, comprising predominantly exotic grass species, are highly altered environments that exhibit limited structural complexity, compared with unmodified habitats. Structural complexity is a key factor influencing reptile richness and diversity (Heatwole & Taylor 1987; Hadden & Westbrooke 1996; Michael *et al.* 2008), so a lack of structural complexity could explain the avoidance of ski runs by lizards. Indeed, the Guthega Skink and Southern Grass Skink are strongly associated with structurally complex habitats (Table 2). Thus, the removal of woody debris, rocks and vegetation from groomed ski runs may explain the infrequent sightings of these species on ski runs (Sato *et al.* 2013b) - especially the Guthega Skink, which shelters in burrows under rocks and shrubs (Green & Osborne 2012; Atkins 2013).

Conversely, both the Alpine She-Oak Skink and Tussock Skink are negatively associated with increasing habitat structure (Table 2), suggesting that the maintenance of structural complexity will not benefit all lizard species. Instead, heterogeneity needs to be maintained across ski resort landscapes to accommodate the requirements of a diversity of reptile species. However, it is important to note that the Alpine She-Oak Skink and Tussock Skink avoided exotic grass ski runs but were prevalent in native sod-tussock grasslands (Sato *et al.* 2013b), indicating that ground layer complexity may be important for these species.

Risk of Predation

Predation risk for reptiles is closely associated with structural complexity because structural features provide lizards with shelter to avoid predation (Webb & Whiting 2005). Conversely, a lack of structural complexity can expose lizards to elevated levels of predation (Amo *et al.* 2007), potentially triggering avoidance of "risky" habitats. In Australian ski resorts, predation risk by corvids was highest on exotic grass ski runs that lizards avoided, and lowest in undisturbed native grasslands (Sato *et al.* 2014). Importantly, predation risk by corvids was significantly reduced on ski runs where grasses were left unmown (Sato *et al.* 2014). This indicates that retaining even low levels of structural complexity on ski runs (e.g. long grass or sections of unmown grass that link habitats with greater structural complexity) will provide some benefit to lizards in ski resorts by decreasing avian predation when lizards use ski runs. Retaining unmown grass also may improve the fitness and body condition of lizards in ski resorts because, with increased cover that provides shelter from predators, individuals will not need to employ energy expensive behaviours (e.g. increased sprint speed and flight distance) to cope with elevated predation risk when crossing ski runs (Amo *et al.* 2007). That said, it is very likely that exotic grass ski runs will remain less useful to reptiles in comparison to the structurally more complex heathlands and tussock-forming grasslands that offer more shelter from predators.

Thermal Regimes

Access to suitable microclimates for basking is important for many reptiles to ensure that body temperature can be effectively regulated (Spellerberg 1972), thereby improving individual physiological, reproductive and ecological performance (Huey 1982). Suitable microclimates vary for individual lizard species, but for Australian alpine/subalpine lizards, non-lethal microclimates are likely to lie between 2.0 and 42.5 °C (see Spellerberg 1972). During the day, mown exotic grass ski runs are often too hot for lizards to use (ground surface temperatures exceed 42.5°C; Sato *et al.* 2014). The hostility of the environment is compounded by the absence of cover objects that lizards could use to shelter from extreme temperatures. If structural complexity (e.g. unmown grasses or patches of remnant vegetation) is retained on ski runs, microclimates in these areas become more favourable. Both unmown ski runs and edge habitats of remnant vegetation retained on ski runs offer lizards warm, but not extreme, microclimates. These altered thermal regimes may enhance thermoregulatory conditions for lizards and encourage the use of ski runs during spring and summer.

Managing Ski Resorts to Enhance Reptile Conservation

While the effects of ski-related disturbances are largely negative for reptiles, lizards still occur in Australian ski resorts, indicating that some species are able to tolerate disturbance to some degree - although tolerance may be minimal for sensitive species. Nevertheless, the almost complete absence of lizards from highly modified ski runs indicates that there is a disturbance threshold above which lizards are unlikely to persist. Thus, there is a need for management strategies to be implemented that facilitate the persistence of alpine/subalpine reptiles in ski resorts. To this end, we suggest several management actions that are based on the factors driving reptile distribution patterns summarised above.

First, given the negative effects that ski-related disturbances have on reptiles, we advocate that undisturbed native vegetation be retained wherever possible in Australian ski resorts. Moreover,

we argue that extensive modification to habitats containing diverse vegetation communities and structural habitat attributes (such as large boulders and logs) be carefully considered as part of development applications. This is because these disturbances are likely to have long-lasting effects on reptile communities, given the slow recovery rates of alpine/subalpine vegetation to disturbance (Illich & Haslett 1994; Urbanska 1997; Scherrer & Pickering 2006) and the fact that boulderfield habitat may take thousands of years to form (Larson *et al.* 2000). Development activities requiring intensive disturbance to alpine or subalpine landscapes, such as the construction of groomed ski runs, terrain parks or half-pipes, should be limited to parts of resorts that are already highly modified.

Second, if native heath cannot be retained when developing new ski runs in Australia, rehabilitation should use locally endemic plant species including grasses (e.g. *Poa costiniana* and *Poa fawcettiae* in NSW), low shrubs [e.g. Mountain Hovea (*Hovea montana*), Alpine Grevillea (*Grevillea australis*) and Dusty Daisy Bush (*O. brevipedunculata*) in NSW) or forbs [e.g. Button Everlasting (*Coronidium scorpiodes*) in NSW] that are unlikely to compromise the safety of skiers (DECC 2007). However, this may not be possible on ski runs with high skier traffic or high densities of beginner skiers. For these ski runs, plantings of 'vegetation corridors' or the introduction of semi-submerged rocks and logs (similar to the wildlife crossings already used by ski resorts; PBPL 2002) between isolated patches of habitat are advised. These types of habitat linkages may provide sufficient cover on ski runs to reconnect the patches and facilitate reptile movements across ski runs during spring and summer. However, the efficacy of this type of management intervention for reptiles requires investigation before implementation as a conservation action in ski resorts.

Third, we recommend that in localities where threatened reptile species are known to occur, the width of highly modified ski runs be reduced through strategic planting of native vegetation on ski runs. For narrow ski runs (<20 m wide), this can be achieved by buffering the edges of the ski runs with native vegetation so that there is a gradual transition between native vegetation

and exotic grasses. For wide ski runs (>30 m wide), we suggest that, in addition to buffering edges, patches of native vegetation containing structural features (such as woody debris) are established on the run to break up the extent of the inhospitable exotic grass matrix. Habitat patches such as these may act as stepping stones for lizards between patches of unmodified habitat (see Lindenmayer & Fischer 2006), but could also offer lizards sufficient resources for permanent inhabitation. It is also possible that small patches may act as predation sinks, where habitat attracts lizards and local predators learn that the patches are profitable foraging areas. Consequently, an important avenue of further research would be to experimentally assess immediate and long-term risks and benefits of restored habitat patches for lizards.

Finally, in areas where it is not possible to revegetate or rehabilitate ski runs, we recommend that mowing or slashing of exotic grasses be ceased to retain sufficient cover to protect lizards from predators and/or extreme thermal conditions. If it is imperative that exotic grasses on ski runs be slashed to facilitate early snow coverage or prevent the encroachment of woody vegetation, we recommend that the mowing be restricted to periods of low lizard activity (i.e. as late as possible in autumn, and no earlier than late April, after reproductive and dispersal activities have taken place; Green & Osborne 2012).

Challenges Affecting the Conservation of Alpine/Subalpine Reptiles

A significant obstacle to the implementation of effective conservation actions for reptiles that occur at high elevations is the limited knowledge about this assemblage. While recent research has yielded important information to direct management, we still have only limited knowledge about the wider spatial distribution of alpine/subalpine reptiles across the Australian Alps, the population dynamics of species inside and outside ski resort lease areas, and the dispersal ability and home ranges of species, including the threatened Alpine She-Oak Skink and Guthega Skink. Without this information, it is difficult to evaluate (i) the extent to which individual ski resort features act as barriers to animal movement that may affect local population persistence, (ii) the

significance of ski resorts in reducing population persistence, particularly of the Alpine She-Oak Skink and Guthega Skink, at regional or national scales, (iii) the positive role that ski resorts may play as unburnt refuges in landscape-scale bushfires when they receive preferential fire protection from conservation agencies relative to the surrounding unmodified habitat, and (iv) the impacts that climate change (including the predicted increase in wildfire frequency; Pickering *et al.* 2004) may have on alpine-subalpine reptiles, and the severity of those impacts.

A second, equally important, factor to consider is the impact of the current development approval process on the conservation of alpine/subalpine reptiles. In NSW, legislation pertaining to ski resort developments does not effectively manage the incremental removal of habitat (i.e. vegetation, soils and/or structural attributes), because each development application is treated independently. Moreover, some development activities are exempt from approvals [see Clause 19, Part 3 of the State Environmental Planning Policy (Kosciuszko National Park - Alpine Resorts) 2007], and variations in the interpretations of this clause can lead to substantial consequences for the environment. Ultimately, the accumulation of small disturbances and incremental removal of important habitat features over time may irrevocably alter the landscape for reptiles, rendering them largely uninhabitable for all but the most disturbance-tolerant, generalist species. Thus, to support the conservation of reptiles in ski resorts - particularly threatened species - the development approval process must consider not only the immediate impact and magnitude of an activity, but also the cumulative effect development proposals may have on alpine/subalpine communities.

Conclusions

Ski-related disturbances have largely negative effects on reptiles because modifications to vegetation composition and structural complexity in alpine/subalpine environments subsequently alter rates of predation and thermal regimes that govern reptile survival. Nevertheless, reptiles continue to persist in some parts of Australian ski resorts, suggesting that

they are resilient to low levels of disturbance. That said, threatened habitat specialists including the Alpine She-Oak Skink and Guthega Skink are usually found only in or very close to minimally disturbed habitat. Thus, the absence of strategies targeting the conservation of alpine/subalpine reptiles (including threatened species such as the Alpine She-Oak Skink and Guthega Skink) requires immediate attention if these animals are to continue inhabiting areas within and adjacent to ski resorts. We broadly recommend that (i) intensive disturbances be restricted to already highly modified areas of Australian ski resorts, (ii) existing native vegetation and structural complexity be retained wherever possible during ski developments, and (iii) structural complexity be re-established at highly modified sites through revegetation programs and the cessation of mowing during peak lizard activity periods. Due to the limited ecological information available to inform management, the national threat status of the Alpine She-Oak Skink and Guthega Skink, and the potential cumulative, and synergistic, impacts of development and climate change on alpine-subalpine reptiles, a precautionary approach to the conservation of alpine/subalpine reptile assemblages is warranted.

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SYNTHESIS

To date, there have been few studies investigating the distributions of Australian alpine-subalpine reptiles, or the processes driving those distribution patterns. Osborne (1983) showed that reptiles within Kosciuszko National Park, in New South Wales, occupy a diversity of habitat types – predominantly snow gum woodlands, wet heathlands and rocky outcrops - that occur both within and outside of ski resort lease areas in Kosciuszko National Park. Since then, studies in Victoria have added to our understanding of the distributions of reptiles across the mainland Australian Alps, showing that the distributions and abundances of dispersal-limited reptile species are likely to be strongly affected, particularly in the short-term, by natural processes such as wildfires (Clemann 2008a), but also by human-related disturbances such as the construction and expansion of ski infrastructure (Clemann 2002; Koumoundouros *et al.* 2009). Moreover, climate change may further restrict the distribution of endemic alpine-subalpine reptiles occurring above 1500 m, including *Cyclodomorphus praealtus* (Alpine She-oak Skink) and *Liopholis guthega* (Guthega Skink), because these species have little scope for uphill migration (Clemann 2008b). Thus, the already threatened *C. praealtus* and *L. guthega* will be increasingly pressured by changes associated with climate change such as alterations to vegetation composition (TSSC 2009; TSSC 2011) and the upward migration of potential predators such as *Dacelo novaeguineae* (Laughing Kookaburra) (Green 2006).

This thesis has built on our current knowledge of the distribution of alpine-subalpine reptiles by focussing on the effects that ski-related disturbances have on reptiles. My research has shown that ski-related disturbances, particularly the creation of ski runs, negatively affect the distribution and abundance of reptiles – even disturbance tolerant species such as *Pseudemoia entrecasteauxii* (Southern Grass Skink). Despite the negative impact that ski-related disturbances have on alpine-subalpine reptiles, reptiles continue to persist in ski resorts in habitats where modifications to vegetation composition are limited and structural habitat

features such as boulders and woody debris are retained. This suggests that these animals can tolerate disturbance to some degree, but are likely to have the best chance of long-term persistence if modifications to existing vegetation composition and habitat structural complexity are minimised. Given the context of Australian ski resorts (i.e. occurring within or surrounded by National Parks that serve to protect biodiversity and ensure sustainable development; DEC 2006), the currently limited ecological information available to inform management of reptiles, the national threat status of two high-altitude endemics (*C. praealtus* and *L. guthega*), and the potential cumulative, and synergistic, impacts of development and climate change on alpine-subalpine reptiles, a precautionary approach to the conservation of alpine-subalpine reptile assemblages is warranted.

To this end, I suggest that the long-term persistence of populations of reptiles in Australian ski resorts can be broadly improved by minimising disturbances to existing habitat, but also by increasing the structural complexity available (i.e. increasing cover) on highly modified ski runs that may be limiting the ability for reptiles to move throughout the landscape. More specifically, management actions aimed at conserving reptiles in ski resorts should involve: (1) restricting intensive ski-related disturbances to already highly modified areas of Australian ski resorts to prevent further disturbance to suitable reptile habitat, (2) retaining existing native vegetation and structural complexity, particularly large rocks (a critical habitat feature for the threatened *L. guthega*), wherever possible during ski developments, (3) re-establishing and maintaining low levels structural complexity at highly modified sites through revegetation of ski runs with native grasses and low-lying shrubs, (4) improving connectedness of isolated, existing reptile habitat through the incorporation of small (> 60 m^2) vegetated habitat patches on ski runs, and (5) ceasing mowing or slashing activities during peak lizard activity periods to facilitate animal movements across ski runs during the spring, summer and early autumn months. Not all actions will necessarily be appropriate for every situation, but combinations of these recommendations – particularly the retention and maintenance of low levels of structural complexity in highly

modified areas of resorts – will facilitate the movement of reptiles throughout modified ski resort landscapes, enhancing the likelihood of their persistence in these areas.

In suggesting these management actions, I acknowledge that further research is required to improve the effectiveness of conservation actions for alpine-subalpine reptiles, largely because of the limited ecological research available for this assemblage. My thesis focussed on four potential factors that can influence the distribution of reptiles – vegetation composition, structural complexity, thermal environments and risk of predation. However, another important determinant of reptile distribution – food availability (Daly *et al.* 2008; Diaz and Carrascal 1991) - was not investigated. Thus, further research should aim to elucidate the dietary requirements of alpine-subalpine lizards, as well as the distribution of prey items within and outside of ski resorts. Currently, species-specific dietary requirements are unknown (alpine-subalpine lizards are assumed to be generalist insectivores; Green and Osborne 2012), as are the impacts of ski resorts on prey (invertebrate) distributions. Another important avenue of research arising from this thesis will be to investigate the efficacy of the management actions I recommended – particularly prior to broad-scale use in Australian ski resorts. This would require the implementation of an experimental monitoring approach of target reptile species (e.g. *C. praealtus* and *L. guthega*) in parts of ski resorts with and without management actions applied. The success of the management actions (i.e. restoration and revegetation activities) could initially be measured by the presence of target species in restored and revegetated parts of ski resorts over repeated survey periods (to account for the fact that the location of or sightings of lizards can vary depending on factors such as time of year, time of day, current and recent weather conditions). However, subsequent measures of effectiveness should look at whether management actions facilitate movement and/or dispersal of target species between habitat patches in ski resorts (i.e. may require a capture-mark-recapture, radio-telemetry or genetic approach). Given that the movement ecology of reptiles in the Australian Alps is largely unknown, it will be important to investigate the dispersal ability and home range sizes of

reptiles both within and outside ski resorts, to determine whether ski resort infrastructure affects (or impedes) the movements of alpine-subalpine reptiles.

In summary, this thesis added to the knowledge we have of alpine-subalpine reptiles in Australia by presenting an in-depth investigation into the patterns of reptile distribution in and around ski resorts, as well as factors that may be driving those observed patterns. It offers land managers strategies that can be implemented to facilitate the persistence of alpine-subalpine reptiles in ski resorts to minimise and potentially mitigate disturbances arising from ski resort management. Ultimately, it also highlights the need to continue building on our knowledge of Australian alpine reptiles - particularly in the face of multiple, potentially interacting factors such as climate change, human disturbances (e.g. ski-related disturbances) and natural disturbances (e.g. wildfires) - in order to maximise the efficacy of actions taken to conserve this unique animal assemblage.

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